

PATTERNS OF UNGULATE MORTALITY AND UNGULATE
MORTALITY PROFILES FROM LANGEBAANWEG (EARLY
PLIOCENE) AND ELANDSFONTEIN
(MIDDLE PLEISTOCENE),
SOUTH-WESTERN CAPE PROVINCE, SOUTH AFRICA

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(With 16 figures and 4 tables)

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ABSTRACT

An ungulate species in which females usually have one young (or less) per year will have a catastrophic (= survivorship = 'lx') age profile with a down-staircase shape in which successively older age classes contain progressively fewer individuals. The corresponding attritional (= mortality = 'dx') profile will tend to be U-shaped, with a large peak in the youngest age class and a second smaller peak beyond 40–50 per cent of potential individual lifespan, or L-shaped, with a large peak in the youngest age class and no obvious peaks thereafter. A species in which females regularly produce more than one young per year will have catastrophic and attritional profiles that both exhibit the down-staircase form. In samples of fossil ungulates, reasonably accurate age (mortality) profiles may be calculated from dental crown heights, using quadratic formulae that assume that the rate of dental wear slows with age. Without sound contextual information, available from Langebaanweg (early Pliocene) but not from Elandsfontein (Middle Pleistocene), age profiles may be difficult to interpret, even when their form (catastrophic v. attritional) is clear. Establishing whether bones accumulated seasonally or not and determining the sex ratio in fossil ungulate samples is far more difficult than establishing age profiles. In conjunction with contextual information, age profiles in fossil samples may be used to infer basic biological facts in a species, such as the common rate of reproduction. The major impediment to broader application of age (mortality) profile analysis in palaeontology and archaeology is the rarity of suitably large samples.

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INTRODUCTION

The purpose of this paper is twofold: first, to review those aspects of ungulate mortality that are of special interest to palaeontologists and second, to construct and interpret ungulate mortality profiles from the fossil sites of Langebaanweg (early Pliocene) and Elandsfontein (mid-Pleistocene) in the south-western Cape Province of South Africa. Both are key sites for understanding Late Cenozoic mammalian evolution in Africa, and much of their importance derives from the fact that they have provided unusually large samples of well-preserved bones. These samples are useful not only for understanding the origins and meaning of the Langebaanweg and Elandsfontein fossil accumulations but also for illustrating the potential and the limitations of mortality profile analysis based on fossil ungulate remains.

Mortality profile analysis is essentially an aspect of the field of population dynamics whose central tool is generally the 'life table' as discussed, for example, by Deevey (1947). The emphasis here, however, will not be on 'life tables' but on mortality profile shape as a means of determining cause of death in fossil samples. The discussion here builds on and expands concepts and insights provided by many other investigators, particularly Deevey (1947) and Spinage (1972a) with respect to mortality patterns in general, and Kurtén (1953) and Voorhies (1969) with respect to mortality patterns in fossil mammals.

SOME GENERAL PRINCIPLES OF POPULATION DYNAMICS
IN LARGE MAMMALS

A convenient way of illustrating some basic principles of large mammal population dynamics is to formulate a hypothetical population such as the one whose age structure is presented in the column labelled 'lx' in Table 1. Maximum individual longevity in this population is 9 years. Each year 500 new individuals are born.

If we require that the overall population size remain constant from year to year, the 500 births will have to be balanced by 500 deaths. If we further require that the age structure remain unchanged, the 500 deaths will have to be strictly apportioned among the various age classes. More specifically, the number of deaths in each age class will have to equal the number of individuals that survive to that age class minus the number that survive to the next age class. The resulting death tallies are listed in the 'dx' column of Table 1, and the relationship between corresponding 'lx' and 'dx' values is illustrated graphically in Figure 1. Although the requirements of a constant population size and constant age structure may appear arbitrary, natural populations adapting to stable environments probably do tend to both a constant size and a constant age structure.

The 'dx' entries in Table 1 are measures of absolute mortality in successive age classes. Dividing each 'dx' entry by its corresponding 'lx' entry provides a

TABLE 1

The age structure of a hypothetical population of large mammals in which females give birth once a year, total births are 500 per year, and potential individual longevity is 9 years.

Age (x) (years)	Number of live individuals (lx)	Number of dead individuals (dx)	Rate of mortality % (qx)
0-1	500	250	50
1-2	250	25	10
2-3	225	22	10
3-4	203	20	10
4-5	183	37	20
5-6	146	44	30
6-7	102	41	40
7-8	61	37	60
8-9	24	24	100
9-10	0	0	

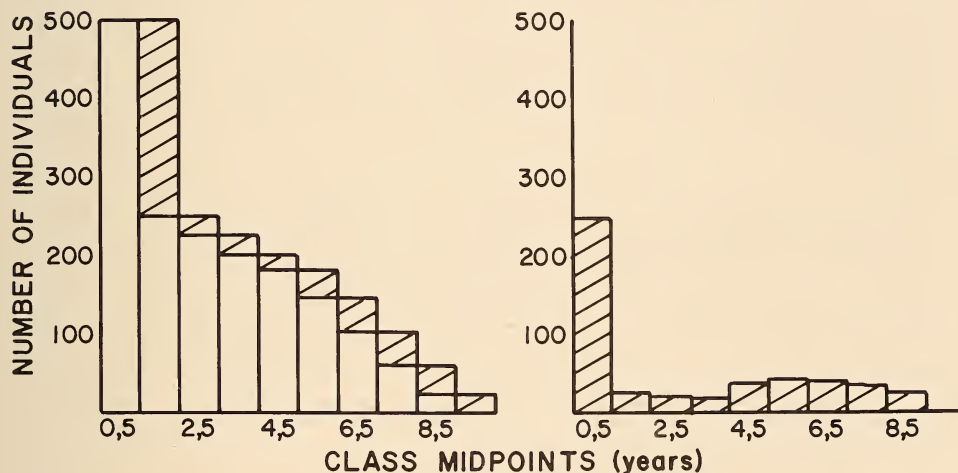


Fig. 1. Left. Blank bars: the age structure of a hypothetical population of large mammals in which females give birth once a year, total births are 500 per year, and potential individual longevity is 9 years. Hatched bars: the number of individuals of each age who must die each year if the population size and age structure are to remain unchanged.

Right: A separate display of the hatched bars, reflecting the age profile of those individuals who die each year in the hypothetical population.

measure of relative mortality or what is commonly called 'the rate of mortality'. Rates of mortality for successive age classes are listed in the 'qx' column of Table 1. In population biology, 'lx', 'dx', and 'qx' are conventional notations for tallies of live individuals, dead individuals, and rates of mortality respectively. When these notations are used, age is designated by 'x'.

As a rule, individual large mammals achieve sexual maturity at an age that is roughly 10 per cent of maximum potential longevity. In our hypothetical

population this would mean that essentially all individuals over 1 year of age would be sexually mature. The total of such individuals (from the 'lx' column of Table 1) is 1 194. Assuming that half of these individuals (597) are female and females can produce only one offspring per year, then 84 per cent of the females ($\frac{500}{597}$) would have to give birth every year to maintain a constant population.

It is interesting to determine what would happen to the hypothetical population if the key constraints were removed. Suppose, for example, that we wanted to force the population into decline. The most direct way would be to increase mortality in the youngest sexually mature age classes. This is because there are only 597 females to produce 500 young every year. Even a slight rise in mortality in the youngest sexually mature age classes would drive the total number of sexually mature females below 500, not only immediately reducing the size of the population but also reducing the number of new births in the coming year. An increase in mortality in the youngest sexually mature females can be particularly disastrous under natural circumstances, since not all sexually mature females in natural populations will actually be capable of breeding. Some will certainly be barren, particularly in the oldest age classes. Often, older individuals also tend to be infirm, so that they suffer higher rates of mortality, a circumstance which has been assumed for our hypothetical population.

If, instead of decline, we wanted to promote population growth, the most direct way would be to reduce mortality in the first age class, since even a small percentage decrease would significantly increase the number of individuals that reach sexual maturity. There would be a cumulative effect, since this would also increase the number of births in the following year. However, even though Table 1 shows that current first-year mortality is 50 per cent, which seems quite high, a reduction in rate may be very difficult to achieve. This is because the very young in many species are extremely vulnerable to death by predation, disease, accidents, starvation, etc. First-year mortality rates in the vicinity of 50 per cent are, in fact, common in many naturally occurring populations of large mammals.

So far we have assumed that each female is capable of producing only one young per year. It is instructive to see what happens if the number of potential young is increased to two per year. A constant population size can now be maintained with only half as many females as before. If, in fact, population size is to remain unchanged, mortality rates must rise in the youngest age classes to reduce the number of sexually mature individuals. Table 2 provides 'lx', 'dx', and 'qx' values for a hypothetical population similar to our original one in constant overall size, but characterized by 1 000 births per year from 500 females. The relationship between corresponding 'lx' and 'dx' values in Table 2 is illustrated graphically in Figure 2.

To summarize, populations of large mammals that are constant in size and age structure will exhibit age profiles in which successively older age classes

TABLE 2

The age structure of a hypothetical population of large mammals in which females give birth twice a year, total births are 1 000 per year, and potential individual longevity is 9 years.

Age (x) (years)	Number of live individuals (lx)	Number of dead individuals (dx)	Rate of mortality % (qx)
0-1	1 000	700	70
1-2	300	150	50
2-3	150	75	50
3-4	75	30	40
4-5	45	9	20
5-6	36	7	20
6-7	29	6	20
7-8	23	12	50
8-9	11	11	100
9-10	0	0	

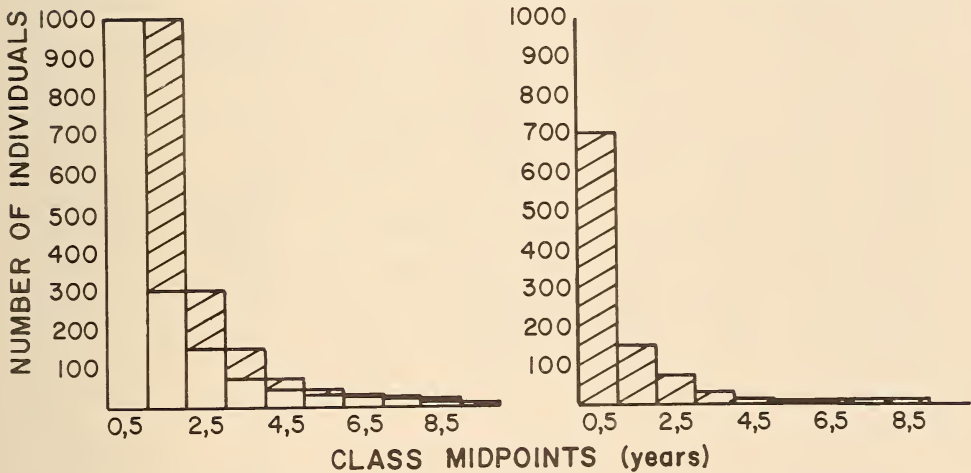


Fig. 2. Left. Blank bars: the age structure of a hypothetical population of large mammals in which females give birth twice a year, total births are 1 000 per year, and potential individual longevity is 9 years. Hatched bars: the number of individuals of each age who must die each year if the population size and age structure are to remain unchanged.

Right. A separate display of the hatched bars, reflecting the age profiles of those individuals who die each year in the hypothetical population.

contain progressively fewer individuals (Figs 1 and 2, left). If the females in the population can have only one young per year, the age profile of those individuals who die each year will generally be U-shaped (Fig. 1, right), reflecting the fact that the rates of mortality are generally highest in the very young and in the old. If, as may be the case in some natural populations, the rate of mortality does not rise sharply in older age classes, the age profile of those individuals who die each year may be L-shaped, with no obvious peaks

after the one in the youngest age class (see below). Whatever the case, however, the age profiles characterizing the live and dead segments of the population in any given year will be formally quite distinct (Fig. 1, left v. Fig. 1, right.)

If the females in the population produce more than one young per year, the age profile of those individuals who die each year will be quite similar in shape to the age profile of those who remain alive, reflecting the fact that rates of mortality remain high into middle life. The main point is that, unlike populations in which females produce only one young per year, the age profiles characterizing the live and dead segments of the population will be difficult, if not impossible, to distinguish on form alone (Fig. 2, left v. Fig. 2, right).

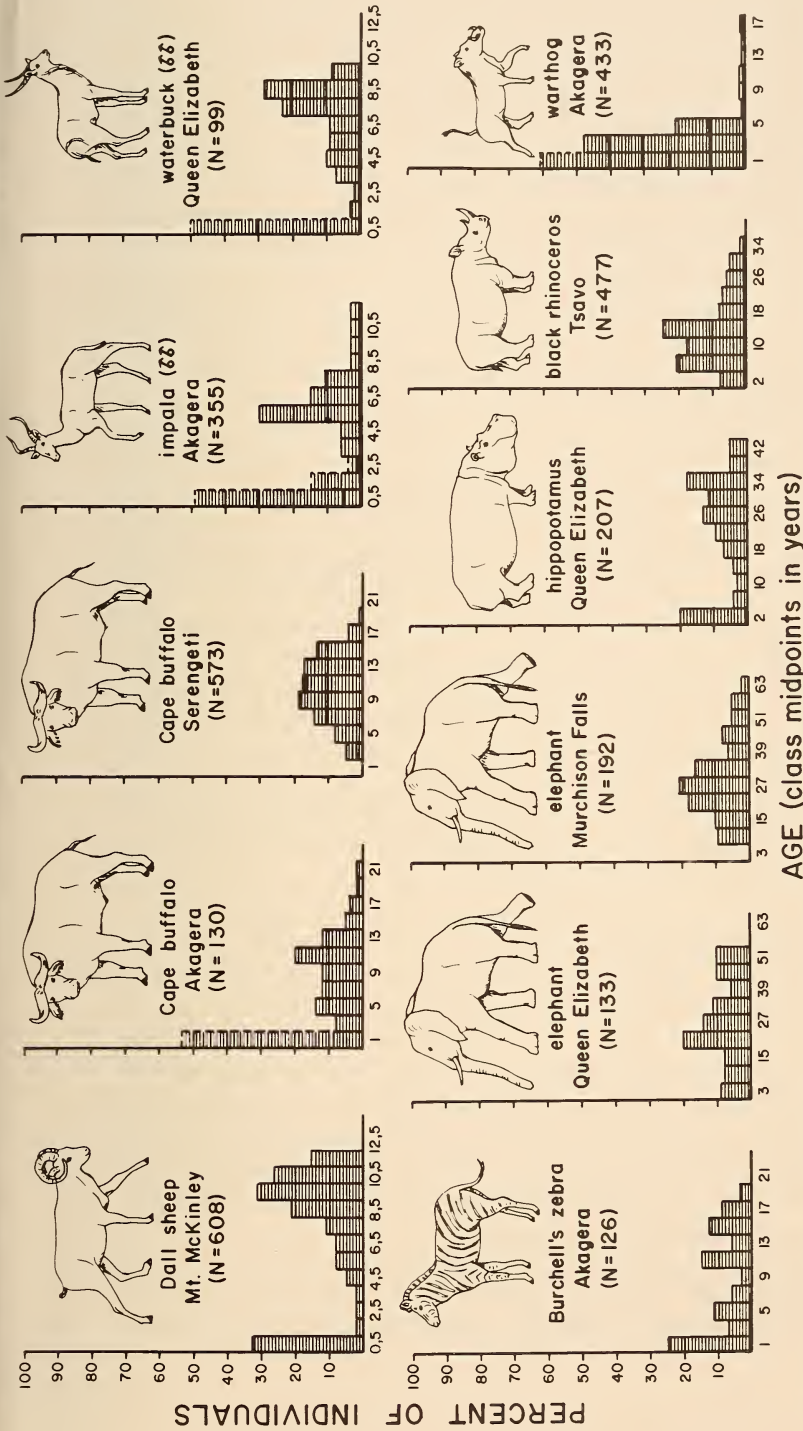
AGE STRUCTURE AND MORTALITY IN EXTANT POPULATIONS OF LARGE MAMMALS

Characteristic age structures and mortality patterns have been established for remarkably few populations of large mammals. One major reason is that many populations are fluctuating rapidly in size or rapidly declining, often as a result of human activity. There is no way of determining the typical age structure and mortality pattern of a population whose overall size is changing rapidly. Another problem is that, even for stable populations, it is difficult to collect reliable data. Three basic methods exist (Deevey 1947). First, survivorship to successive age classes may be recorded in a cohort of individuals born at more or less the same time; second, a census may be conducted of all those individuals alive at any one time; and third, individuals that die within a restricted time may be aged and tallied. In the conventional terminology of population biology, the first two methods produce 'lx' data, while the third produces 'dx' data. In theory, all three methods will provide the same age structure and mortality pattern for a population with a fixed size and age structure.

In practice, the first method—tallying the numbers of individuals from a single birth cohort that survive to successive ages—is all but impossible to apply to free-ranging populations of large mammals. It will also not yield results quickly, since individual large mammals have relatively long potential lifespans.

The second method—live censusing—is more practical, but it requires either that an entire population be studied or that there be some way of obtaining a reasonably large, unbiased sample. It further requires a method for ageing live individuals reliably, often only by observing them from a distance. The third method—tallying deaths—is, in fact, usually the most practical, since it may be based on skeletal material, which is relatively easy to sample and age.

Some representative mortality ('dx') profiles obtained by the death-tally method are presented here in Figure 3. All the profiles have been cast so that the number of age classes in each is approximately equal, while the second age class generally contains the youngest sexually mature individuals. Each profile



MORTALITY ('dx') PROFILES IN SOME POPULATIONS OF FREE-RANGING LARGE MAMMALS.

Fig. 3. Representative mortality profiles in populations of free-ranging large mammals. The profiles have been cast so that the number of age classes is approximately the same in each. All the profiles are based on systematically collected skulls or jaws from populations that were at least roughly stable in size and age composition during the period when mortality took place. In all the profiles, very young individuals (in the first age class) are underrepresented because their skeletal remains are more likely to disintegrate before recovery. Dotted bars in the profiles for the Cape buffalo, impala, and wart-hog from Akagera National Park indicate the original analyst's attempt to use observations on live populations to 'correct' the underrepresentations of very young individuals.

Sources: Dall sheep (*Ovis dallii*) in Mount McKinley National Park (Murie 1944); Cape buffalo (*Syncerus caffer*), impala (*Aepyceros melampus*), Burchell's zebra (*Equus burchelli*), and wart-hog (*Phacochoerus aethiopicus*) in Akagera National Park (Spinage 1972a); waterbuck (*Kobus ellipsiprymnus*) in Queen Elizabeth Park (Spinage 1970); Cape buffalo in the Serengeti National Park (Sinclair 1977); elephant (*Loxodonta africana*) in Queen Elizabeth and Murchison Falls Parks (Laws 1966); hippopotamus (*Hippopotamus amphibius*) in Queen Elizabeth Park (Laws 1968); and black rhinoceros (*Diceros bicornis*) in Tsavu National Park (Goddard 1970).

is based on systematically collected skulls or jaws from individuals that died of 'natural' causes such as predation, accidents, and endemic diseases. Age was established by counting the annual rings on horns (Dall sheep) or by estimation from dental eruption and wear (remaining species). The base populations differ in the extent to which they were stable in overall size and age structure during the period when mortality took place, but all approximated stability sufficiently for present purposes.

Very young individuals (in the first age class) are underrepresented in all the profiles, because their skulls are more fragile than those of older individuals. The extent of underrepresentation probably varies from profile to profile depending upon local preservational conditions and on differences among species in skull architecture. Dotted bars in Figure 3 indicate the original analyst's attempts to 'correct' for underrepresentation of the very young in the mortality profiles of buffalo (at Akagera), impala, waterbuck, and wart-hog.

Keeping in mind the universal, though not necessarily equal, underrepresentation of very young individuals, the profiles of all the species but wart-hog are broadly similar in form, suggesting that in each case very young individuals and older adults suffer substantially higher rates of mortality than do younger (young sexually mature) adults. The pattern is very similar to the 'dx' (mortality) pattern in the hypothetical population of Figure 1 (right), in which females were assumed to have no more than one young per year.

In all the species but wart-hog, females also have no more than one young per year, and it was with these real species in mind that the hypothetical population was devised. The 'real' profiles suggest that species in which females bear one young (or less) per year are, in fact, often characterized by especially high rates of mortality among the very young and the old. It is possible, however, that the definition of 'old' may vary from population to population. Figure 3 suggests that in Dall sheep, waterbuck, and hippopotamus a substantial increase in the rate of mortality occurs in adults that are at 60–70 per cent of potential lifespan, while in the other species it tends to occur among somewhat younger adults at about 40–50 per cent of potential lifespan. Many more observations will be necessary to determine if this difference and other apparent differences among the profiles are real, perhaps due to differences in environment or species biology, or whether they are spurious, perhaps due to chance ('sampling error'), to differences in the extent to which the various populations were truly stable, or to differences in the extent to which individuals in different species can be accurately aged from skeletal remains. Since mortality patterns may differ somewhat between males and females in the same population (e.g. Spinage 1970 on waterbuck, or Sinclair 1977 on buffalo), it is further possible that some of the differences among profiles in Figure 3 reflect differences in the sex composition of the samples.

The wart-hog mortality profile is radically different from all the others in that it indicates very high mortality rates not only for very young individuals but also for young (sexually mature) adults. As the original analyst (Spinage

1972a) points out, the distinctive pattern of the wart-hog profile almost certainly reflects the fact that, unlike females in the other species, wart-hog females regularly produce more than one young per year (the common pattern is for a litter of 2 to 7). The wart-hog profile is, in fact, very similar in shape to the 'dx' (mortality) profile of the hypothetical population in Figure 2 (right) in which females were assumed to produce more than one young per year.

Though often less reliable than death-tally profiles such as those in Figure 3, live censuses of large mammal populations support the generalizations that the death-tally profiles suggest. A representative 'census' based on non-selective shooting and observations of live female Himalayan thar (*Hemitragus jemlahicus*) in New Zealand (Caughley 1966) is presented in Figure 4 (left). The population was probably roughly stable in size and age structure when the 'census' was taken. Female thar generally have no more than one young per year, and the inferred mortality ('dx') profile is obviously broadly similar to that of the species in Figure 3 in which females also have one young (or less) per year.

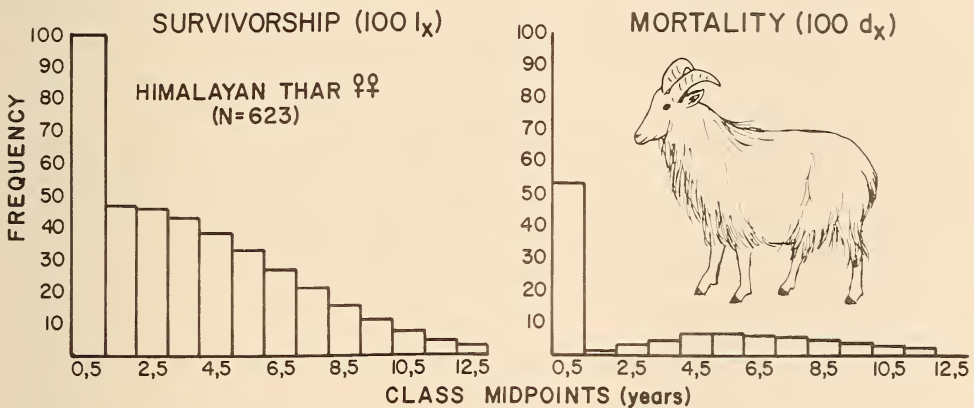


Fig. 4. Survivorship (' l_x ') and mortality (' d_x ') profiles in a population of female Himalayan thar (*Hemitragus jemlahicus*) in New Zealand, as reported by Caughley (1966). The survivorship profile is based on random shooting and live counts, while the mortality profile was inferred from the survivorship count. The mortality profile exhibits a tendency for the rate of mortality to rise fairly sharply in individuals at 40–50 per cent of potential lifespan.

In sum, the available data on extant large ungulate populations suggest that ones in which females have one young (or less) per year will tend to exhibit a mortality pattern in which the rate of mortality is much higher in very young individuals and in older adults than in younger ones. Depending upon the population, 'older' adults may be ones at an age between 40–50 per cent and 60–70 per cent of potential lifespan. The live (' l_x ') age structure of such a population will be similar to that of the hypothetical population of Figure 1 (left), with a shape similar to a down staircase in which a very steep first step is followed by a series of much less steep but steadily steepening ones. The

mortality ('dx') profile of the population will tend to be U-shaped as in Figure 1 (right).

The limited data presented here on large mammals that have more than one young per year may be supplemented by data on fast-breeding small mammals (references in Spinage 1972a) to support the conclusion drawn here that high mortality rates will persist into young adult classes in such populations. The live age structure of the population will be similar to that of a down staircase in which the initial three or four very steep steps are followed by a series of barely perceptible ones. The corresponding mortality profile will recall a very similar staircase, though the very last, barely perceptible, steps will tend to ascend rather than descend (Fig. 2, right). Since the difference in shape between the corresponding live ('lx' or survivorship) and death ('dx' or mortality) profiles is so subtle, a very large sample will be necessary to show which profile is represented by an age structure drawn from material whose context did not allow an a priori determination. The significance of this point will become clear below.

AGE STRUCTURE AND MORTALITY IN SOME FOSSIL POPULATIONS OF LARGE MAMMALS

There is a sense in which the age profile of a fossil population is always a mortality or 'dx' profile, since the individuals involved are all dead. However, it will only resemble the 'dx' profile of an extant population if the fossil individuals died as a result of accidents, predation, endemic disease, and other routine attritional factors that ordinarily have their greatest impact on the very young and the old. If, instead, the fossil individuals died as the result of a great flood, volcanic eruption, epidemic disease, or other catastrophic event that affected individuals of all ages to the same extent, the mortality profile of the fossil population will directly reflect its original live age structure. In other words, it will, in fact, be a survivorship or 'lx' profile. In practice then, the age profile of a fossil population may reflect either mortality ('dx') or survivorship ('lx') as they are commonly defined.

The observations on extant populations presented in the last section suggest that shape alone may be sufficient to determine whether a large mammal mortality profile reflects catastrophic ('lx') or attritional ('dx') mortality, at least in species where females commonly have one young or less per year. In such species a 'catastrophic' (= survivorship = 'lx') profile will tend to be shaped like a down staircase, with the first and near-last steps being the steepest. An 'attritional' (= true mortality = 'dx') profile will tend to be U-shaped, with a large peak or mode in the youngest age class, followed by a marked dip, and then a second, smaller peak in individuals at 40-50 per cent to 60-70 per cent of potential longevity.

In many instances, it is, of course, possible to infer mode of death (catastrophic or attritional) independently of profile shape. For example, cata-

strophic death by drowning is a likely explanation for a fossil example derived from ancient fluvial deposits packed with bones belonging mainly to only one or two species. Catastrophic death is probably also implied in most cases where an age distribution is clearly discontinuous, that is, composed of discrete age classes, each separated from the next by an age gap into which no individuals fall. This could happen only if birth and death were both seasonally restricted events, and a priori, seasonally restricted death (perhaps by flood or brush fire) is more likely to be catastrophic than attritional. This is particularly true if the dead animals accumulated in a deposit over a period of several years, so that their deaths had to occur in the same season each year.

Since it is often possible to infer mode of death (catastrophic or attritional) in a fossil sample by criteria other than age profile shape, age profiles in fossil samples may be used to help establish the general characteristics of survivorship and mortality in large mammals. In this regard they may even prove more suitable than many samples from extant populations, since they are often larger (or can be enlarged quickly with relatively little effort) and they frequently derive from a substantial period of time during which short-term fluctuations in population size and age structure will tend to have cancelled each other out. This means that a fossil sample is more likely to produce an age profile that is truly typical of the population.

Unquestionably the most famous studies of age structure and mortality in fossil populations of large mammals are those by Kurtén (1953) and Voorhies (1969) on samples from late Miocene fluvial deposits in north China and Nebraska respectively. Voorhies carefully excavated his sample himself, while Kurtén analysed material collected by others under conditions that were probably much less well controlled. There is no reason to suppose, however, that collecting seriously biased the age profiles of any of the species that Kurtén studied.

Voorhies's sample was heavily dominated by the extinct pronghorn antelope *Merycodus furcatus*, with the three-toed horse *Protohippus* cf. *perditus* a distant second, and other species still less common. Kurtén's samples came from several localities, at each of which one species tended to dominate heavily, though not necessarily the same species at each locality. In their analyses of dental eruption and wear in the principal species in their samples, both Kurtén and Voorhies found that individuals fell into discrete age modes or clusters, each cluster probably representing a cohort of individuals born at more or less the same time and killed more or less simultaneously. Together with the sedimentary context, this indicates that mortality in the various species studied by Kurtén and Voorhies was 'catastrophic' rather than 'attritional'.

The catastrophic ('lx') profiles of *M. furcatus* and *P.* cf. *perditus* from Nebraska and of the ovibovine bovids *Plesiaddax depereti* and *Urmiatherium intermedium* and the gazelle *Gazella dorcadoides* from north China are displayed on the left-hand side of Figure 5 here. In *M. furcatus* the youngest individuals represented were already old enough at death for their jaws to be

about as durable as those of adults. As a consequence, there is no reason to suppose serious underrepresentation of very young *M. furcatus* in the age profile. In the other four species, however, the jaws of individuals in the youngest (first) age class, and in the ovibovines also in the second age class, were relatively fragile, and such individuals are probably seriously underrepresented in the age profiles. The dotted bars in Figure 5 represent the present writer's attempt to correct for this underrepresentation in the gazelle and ovibovine profiles by assuming roughly 50 per cent first-year mortality in all three species and roughly 10 per cent second-year mortality in the ovibovines. In all five species involved, females probably had no more than one young a year. Keeping in mind that very young individuals are seriously underrepresented in four of the profiles, they are all very similar in form to those of extant species with the same reproductive potential.

The 'dx' profiles that are inferable from the 'lx' ones are shown on the right-hand side of Figure 5. They are also broadly similar to the 'dx' profiles of the extant species, though in general they do not exhibit a clear second peak among older individuals. The absence of a clear second peak may reflect chance ('sampling error') or it may indicate that in some populations of large mammals the rate of mortality does not rise sharply among older adults, leading to an L-shaped (v. U-shaped) shaped mortality profile. The possibility that 'dx' profiles may be L-shaped is not widely recognized but must clearly be borne in mind when interpreting mortality profiles such as those from Langebaanweg and Elandsfontein considered below.

AGE PROFILES PRODUCED BY PREDATION ON SOME POPULATIONS OF LARGE MAMMALS

Figure 6 presents age profiles of Burchell's zebra and Cape buffalo killed by lions on the Serengeti Plain (Schaller 1972), of chamois (*Rupicapra rupicapra*) shot by recent hunters in the Alps (Kurtén 1953 using data from Bourlière 1951), and of pronghorn antelope (*Antilocapra americana*) killed by the late prehistoric occupants of the Eden-Farson site, Wyoming (Nimmo 1971; Frison 1978a). In each case, individual age was established from dental eruption and wear. Very young zebra, buffalo, and chamois are all seriously underrepresented in Figure 6. Lions consume very young zebra and buffalo too quickly and completely for observers to estimate accurately the number of very young killed, while the hunters who shot the chamois were not interested in very young animals because they make poor trophies. If it had been possible to record all kills of zebra and buffalo, very young individuals would certainly be the best represented age class in the kill profiles. Similarly, very young animals would have been the most common individuals in a completely random shot sample of chamois. Only in the pronghorn kill sample, derived by careful excavation of well-preserved bone, are very young animals probably present in more or less their proper proportion.

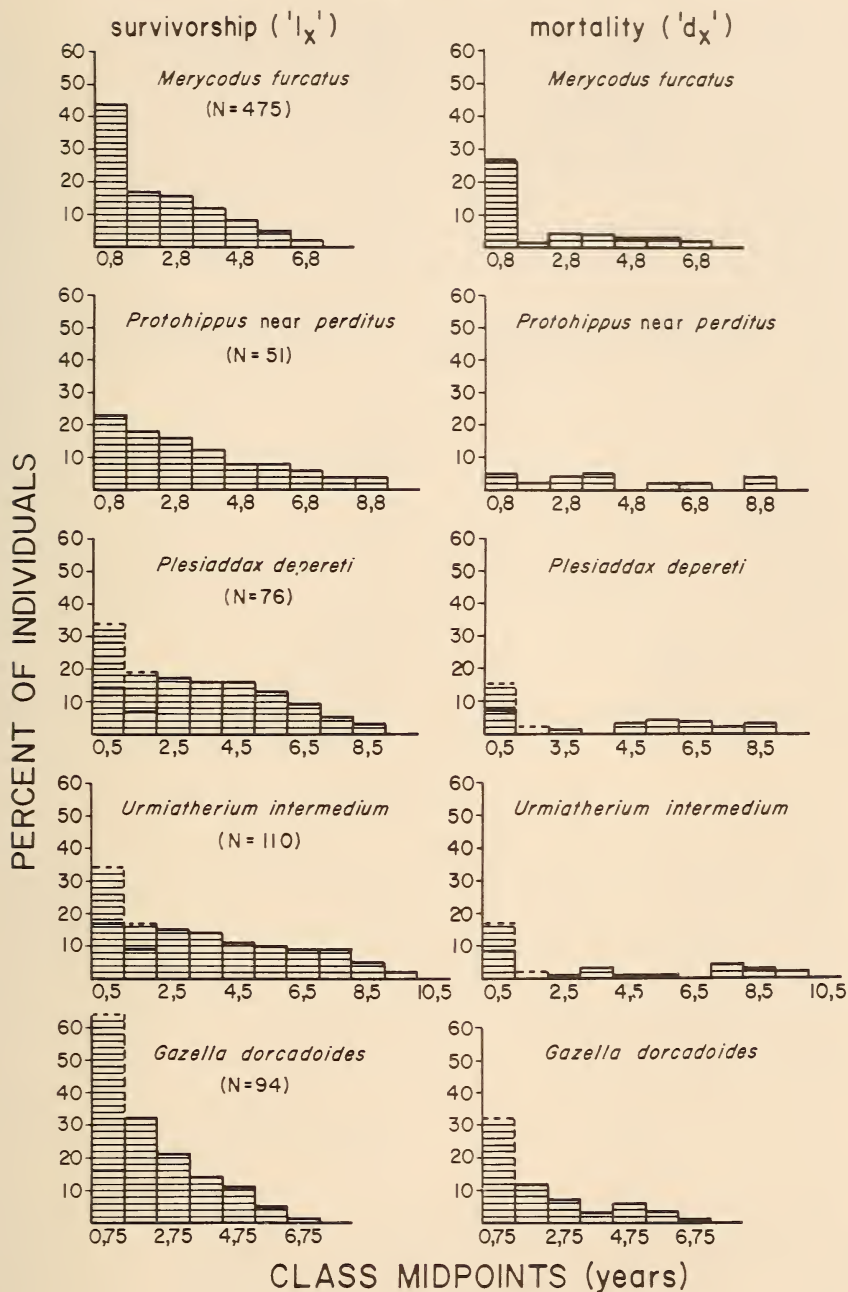


Fig. 5. Catastrophic (= survivorship = ' l_x ') profiles (left) and attritional (death = ' d_x ') profiles (right) in *Merycodus furcatus* and *Protohippus near perditus* from late Miocene deposits at Verdigre Quarry, Nebraska (Voorhies 1969), and in *Plesiaddax depereti*, *Urmiatherium intermedium*, and *Gazella dorcadoides* from various late Miocene localities in north China (Kurtén 1953). The dotted bars represent the present author's attempts to 'correct' for the underrepresentation of young individuals in the profiles of the north Chinese species. In general, the 'death' (= ' d_x ') profiles in this Figure contrast with those in Figures 3 and 4 in lacking a clear second peak among older adults. This may be due to chance, or it may indicate that such a peak is not a necessary feature of attritional mortality in large mammals.

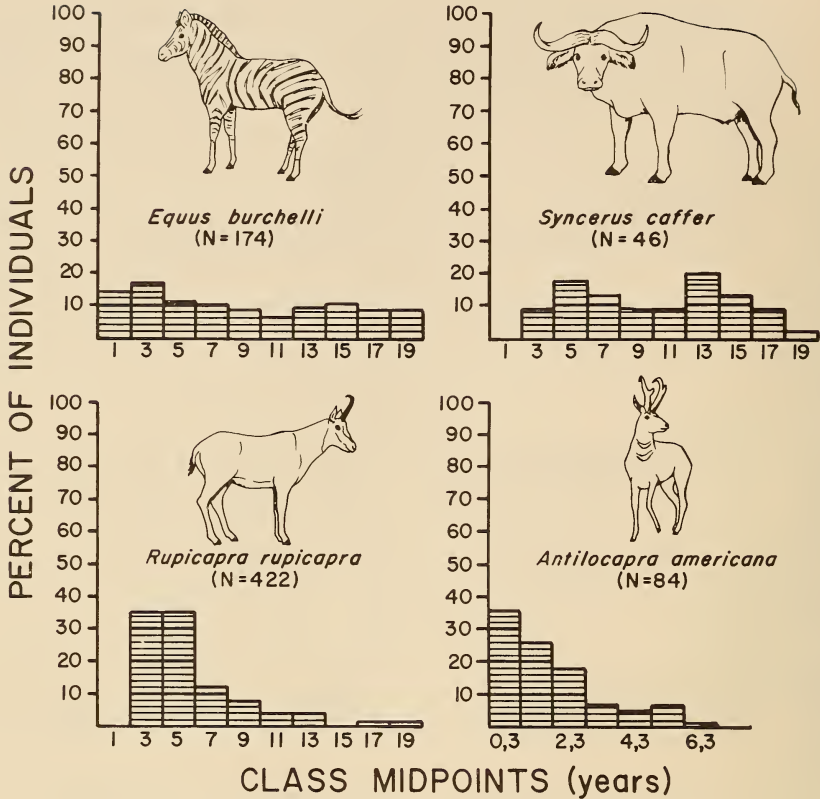


Fig. 6. Age profiles resulting from predation by lions on Burchell's zebra and Cape buffalo (Serengeti Plain) (Schaller 1972); from unrestrained, non-selective shooting of chamois in the Alps (Kurtén 1953 using data from Bourlière 1951); and from prehistoric American Indian hunting of pronghorn antelope (Eden-Farson site, Wyoming) (Nimmo 1971). The numbers of very young zebra and buffalo killed by lions cannot be accurately estimated, but very young individuals would certainly dominate the kill profiles if accurate counts could be made. The hunters who shot the chamois essentially ignored very young individuals because they do not make good trophies. Only in the pronghorn profile are very young animals probably represented in more or less their proper (true) proportion.

The zebra data have been reorganized from the original presentation, with individuals in what were sometimes broader age classes distributed evenly among the two-year age classes used here. All other data are as presented in the original sources.

In all four species, females generally bear no more than one young per year, which means that the profiles in Figure 6 are best compared with those in Figure 1, representing catastrophic (= 'lx' = survivorship) and attritional (= 'dx' = mortality) profiles of a hypothetical population with the same basic reproductive potential. Taking into account the severe underrepresentation of very young individuals in the zebra, buffalo, and chamois profiles, and assuming that attritional profiles need not display a sharp rise in the rate of mortality

among older individuals, the zebra and buffalo profiles are essentially attritional, while the chamois and pronghorn ones are clearly catastrophic.

The reason that the buffalo profile has an attritional shape is because the physical condition, large size, and social organization of young adult buffalo make them largely immune to lion predation. When lions hunt buffalo they are forced to concentrate on the very young and the old. It is probable that similar features of size, condition, and social organization also make young adult zebra less vulnerable to lion predation, though the difference in shape between the zebra and buffalo profiles in Figure 6 suggests the possibility that lions find it easier to kill young adult zebra than young adult buffalo. Whatever the case, lions apparently kill zebra and buffalo of various ages in broadly the same proportions as they would die anyway. Such a pattern of predation is perhaps to be expected in a situation where predator and prey populations have long coexisted, since the prey populations could sustain it indefinitely.

In contrast to the attritional shapes of the zebra and buffalo profiles, the catastrophic shape of the chamois profile reflects the activity of a predator (men with rifles) that was not forced to concentrate on any particular age class. In further contrast to predation on the zebra and buffalo, predation on the chamois could not have continued indefinitely. This is because the elimination of so many reproductively active young adults would depress the birthrate, leading to a decline in numbers and perhaps even extinction. In fact, historic observations indicate that hunting did seriously reduce the chamois population on which the profile in Figure 6 is based.

The method by which the pronghorn were hunted must be inferred, since it could not be directly observed. Given aboriginal American hunting technology, the method most likely to produce a catastrophic profile would be the communal drive, which was, in fact, observed ethnohistorically among Indians hunting pronghorn (Frison 1978*a*). As in the case of the chamois, a method netting so many young (sexually mature) adults would lead to a significant decline in overall pronghorn population size, if it were relentlessly employed. Historically, drives did apparently eliminate local pronghorn populations, which then took several years to recuperate through immigration from neighbouring regions. The point to be made is that hunting methods resulting in catastrophic kills must be restrained, voluntarily or otherwise, if they are not to reduce prey and thus ultimately predator numbers.

In sum, the examples presented here show that predation may produce either attritional ('dx') or catastrophic ('lx') mortality profiles in prey, depending upon the characteristics of prey and predator. An attritional profile, indicating that the predator was largely restricted to very young and old individuals, is perhaps to be expected in any situation where predator and prey have long coexisted. Catastrophic prey profiles, indicating that the predator possessed a capture method to which individuals of all ages were about equally vulnerable, will generally reflect unstable predator-prey relationships, probably mainly ones in which recent people were the predators. If methods leading to

catastrophic kills are not restrained, they can be counter-productive, since they will eventually cause prey populations to decline or even disappear.

ESTIMATING THE AGE OF A FOSSIL UNGULATE AT DEATH

In general, the most useful skeletal elements for estimating the age of individual ungulates at death are the teeth. In many species the age of a recently dead (or still living) individual may be estimated by counting the number of 'annuli' in the cementum covering dental roots (see Morris 1972 or Spinage 1973 for overviews). The cementum annulus method is generally not useful for estimating the age at death of fossil individuals, however, because fossil cementum often does not retain the annulus structure, at least in a way that can be detected with standard preparation techniques (Spiess 1979). Additionally, specimen preparation is destructive, rendering teeth all but useless for further study.

With fossil teeth, the only truly practical method of estimating individual age is to evaluate the state of eruption and wear. This can be done subjectively by comparing fossil dentitions to ones from known-age individuals, if a species is still extant, or objectively by measuring a dental dimension that clearly changes with age. In some fossil samples, such as those studied by Kurtén (1953) and Voorhies (1969), the seasonally restricted birth and death of the species involved allows subjective arrangement of the dentitions into a series of discrete eruption and wear classes. These reflect discrete age clusters, each separated from the last by approximately one year. Assuming that the youngest age class is made up of individuals in the first year of life, it is then possible to assign approximate (modal) ages to each of the successive eruption and wear classes.

In general the subjective method of age determination has the disadvantage that different investigators may estimate different ages from the same fossil dentition and also that it usually requires complete demi-mandibles or maxillae. In many, perhaps most, fossil samples, many individuals are represented only by isolated teeth. The objective method, based on measurement, has the advantage that it produces easily replicable results. Perhaps even more important, it can also be readily applied to isolated teeth, as long as their former position in the mouth can be determined. In sum, for fossil material, the measurement method of estimating individual age from teeth is almost certainly the best. At least with regard to high-crowned ungulates, the most obvious dental dimension to measure is crown height.

The mathematical relationship between advancing age and decreasing crown height has not been thoroughly established for any high-crowned ungulate species. The principal reason is the rarity of large samples of known-age dentitions, particularly ones from a wide variety of age classes. In the absence of a sound body of empirical observations the estimation of age from crown height requires some 'theoretical' assumptions on the nature and rate of crown attrition. In work to this point, the author has made the following assumptions:

1. That reduction in crown height is roughly constant through the life of a tooth, that is, that the relationship between decreasing crown height and advancing age is approximately linear.

2. That for a deciduous tooth, the chronological age of complete crown reduction—when the crown is all but worn away—is the age when the tooth is replaced by its permanent counterpart. For a permanent tooth, the chronological age of complete crown reduction is the age past which no individuals survive in the wild, sometimes known as 'potential ecological longevity'. For most species, the dental eruption and replacement schedule and potential ecological longevity may be obtained directly from wildlife biology publications or indirectly by inference from publications on closely related species of similar size.

3. That the amount of crown height lost per unit time on a deciduous tooth equals the initial unworn crown height divided by the time interval between age of eruption (usually birth) and age of replacement by a permanent tooth. The amount of crown height lost per unit time on a permanent tooth equals the initial unworn crown height divided by the time interval between age of eruption and age of potential ecological longevity. Initial unworn crown height may usually be estimated from unworn or lightly worn teeth occurring in any sample that is large enough to warrant mortality profile construction. In the author's experience, individual variability in unworn crown heights within a local population of a species tends to be very limited, so that the mean of a fossil sample is an adequate estimate, even if it is based on very few specimens.

Klein *et al.* (1981) showed that these assumptions lead to the following age-prediction formulae:

for a deciduous tooth:

$$\text{AGE} = \text{AGE}_s - (\text{AGE}_s / \text{CHO}) (\text{CROWN HEIGHT})$$

for a permanent tooth:

$$\text{AGE} = \text{AGE}_{\text{pel}} - ((\text{AGE}_{\text{pel}} - \text{AGE}_e) / \text{CHO}) (\text{CROWN HEIGHT})$$

where AGE_s is the age at which a deciduous tooth is shed, AGE_e is the age at which a permanent tooth erupts, AGE_{pel} is the age past which no individuals appear to survive in the wild ('potential ecological longevity'), and CHO is initial (unworn) crown height.

Among the various assumptions perhaps the most questionable one is that the rate of crown attrition is constant throughout the life of a tooth. Various studies have suggested that wear is more rapid early in the life of a tooth than later on (see, for example, Grimsdell 1973 on extant Cape buffalo, or Kurtén 1953 and Voorhies 1969 on the fossil ungulate species whose age profiles are presented in Figure 5). Spinage (1971, 1972*b*, 1973) has pointed out that known changes in occlusal topography—roughest at the very beginning, smoothest near the end—imply that attrition will slow with age. Only in mid-life, when the topography tends to remain relatively constant, will attrition occur at a more or less constant rate. In order to accommodate a variable rate of wear of the kind

the changes in occlusal topography suggest, Spinage has proposed age estimation formulae that have the following form, when they are expressed using the terms above:

for a deciduous tooth:

$$\text{AGE} = \text{AGE}_s ((\text{CROWN HEIGHT} - \text{CHO})/\text{CHO})^2$$

for a permanent tooth:

$$\text{AGE} = (\text{AGE}_{pe} - \text{AGE}_e) ((\text{CROWN HEIGHT} - \text{CHO})/\text{CHO})^2 + \text{AGE}_e$$

In a study involving a relatively large sample ($N = 170$) of known-age wapiti (*Cervus elaphus canadensis*), Klein *et al.* (in press) found that Spinage's formulae do, in fact, provide more accurate age estimates from crown height than do the formulae based on a constant wear rate. Perhaps even more important, Spinage's formulae tend to underestimate true age about as often as they overestimate it, while the linear formulae mostly overestimate it. In the language of statistics Spinage's formulae are much less biased estimators. The important point is that they are more likely to produce a truly accurate age profile from a sample of crown heights, since overestimated ages would tend to be balanced out by underestimated ones.

The principal disadvantage of Spinage's formulae is that they are more cumbersome to calculate than those based on a constant wear rate. However, this is not a serious problem if a programmable calculator or computer is available. An additional problem is that changes in the values assigned to the constants AGE_s , AGE_e , AGE_{pe} , and CHO in Spinage's formulae have a greater effect on estimated ages than do comparable changes in the linear formulae. This means that the values of the constants must be selected as carefully as possible when Spinage's formulae are applied.

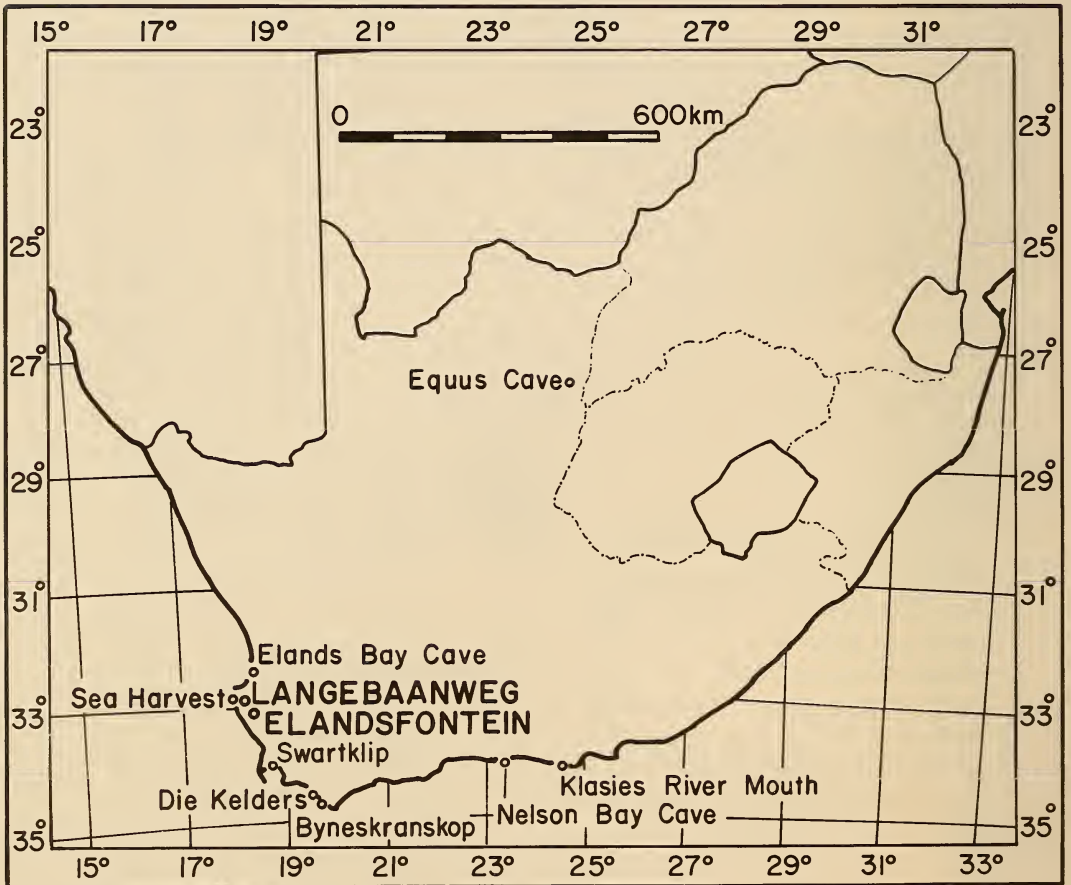
Whichever formulae are used, it is advisable to group the ages estimated from crown heights into classes that are at least as broad as the average error in age estimation. In virtually all instances, a class interval based on 10 per cent of potential ecological longevity will probably suffice. An important characteristic of such an interval is that age profiles based on it will be immediately comparable even among species with very different potential longevitys.

In the case of species such as wapiti in which potential lifespan (AGE_{pe}) is long relative to initial (unworn) crown height (CHO), both the linear and Spinage's formulae will produce quite similar age profiles, when the class interval is 10 per cent of potential lifespan, especially if the permanent tooth used to estimate age is one whose crown height is still measurably greater than '0' when potential longevity is approached. In most species, the tooth that meets this requirement best is the third molar (M3). In very hypsodont species such as equids in which potential lifespan is much shorter relative to initial (unworn) crown height, the linear formulae and Spinage's formulae may produce quite different age profiles, regardless of what tooth is used (Fig. 7). In the case of such species it is imperative that Spinage's formulae be used or the age profiles that result may be quite misleading.

All the age profiles presented below were calculated using Spinage's formulae. For the sake of consistency, some age profiles that were presented in a previous paper where the linear formulae were used (Klein 1981a), have been recalculated, even though their essential form remains the same, since the species involved were low-crowned relative to potential lifespan. All calculations were performed on an IBM Personal Computer.

THE LANGEBAANWEG FOSSIL SITE

Langebaanweg (32°58'S 18°9'E) is located approximately 110 km north-north-west of Cape Town (Fig. 8). Fossils were first reported from Langebaanweg in 1958 (Singer & Hooijer 1958; Singer 1961). In 1969 Q. B. Hendey of the South African Museum initiated a research programme at the site, which has led to a vast accumulation of vertebrate fossils belonging to more than 150



Map showing the approximate locations of sites mentioned in the text.

Fig. 8. The approximate locations of the sites mentioned in the text.

species, primarily mammals and birds. Publications on the site include numerous taxonomic and phylogenetic studies by Hendey and others, and overviews focusing on geologic context and palaeoecology (Hendey 1981*a*, 1981*b*, with references).

The overwhelming majority of Langebaanweg fossils, including all those considered here, come from the Quartzose Sand Member (QSM) (older) and Pelletal Phosphorite Member (PPM) (younger) of the Varswater Formation, as exposed in Langebaanweg 'E' Quarry. There are no materials suitable for chronometric dating, but Hendey's analysis of the Langebaanweg stratigraphic succession in relation to global sea-level and climatic events, together with the vertebrate taxa represented, indicate that the QSM and PPM both accumulated approximately 5 million years ago, or during the early Pliocene as this term is presently defined.

The QSM consists primarily of fine-grained, white quartz sands laid down on the estuarine floodplain of a river that probably entered the sea just to the south-west of 'E' Quarry. The PPM consists of relatively coarse well-sorted sands laid down primarily in the channel of the same river as its bed moved progressively northward. Within the PPM there are two distinct, especially fossiliferous channel fills, known as bed 3aS (further south) and bed 3aN (further north) respectively.

Essentially the same mammalian taxa occur in both the QSM and the PPM, but their mode of occurrence and their relative abundance differ dramatically between the two units. In the QSM partial, semi-articulated skeletons are common and abraded bones are rare. In the PPM partial, semi-articulated skeletons are rare and abraded bones are common. In the QSM several species are more or less equally represented, with no single species dominating overwhelmingly. In the PPM alcelaphine antelopes (*Damalacra acalla* and *D. neanica*) and giraffids (*Giraffa* sp. and especially *Sivatherium hendeyi*) are superabundant compared to all other species, the alcelaphines dominating particularly in bed 3aS and the giraffids in bed 3aN.

In an earlier paper Klein (1981*a*) showed that various species in the QSM are characterized by attritional mortality profiles, while the superabundant giraffids of bed 3aN are characterized by catastrophic profiles. Together with the sedimentary context and mode of fossil occurrence, the mortality profiles clearly suggest that individuals represented in the QSM died mainly of attritional factors such as predation, accidents and endemic disease. Subsequently, their skeletons were disarticulated and partially removed or destroyed by scavengers and other biological agents, but the bones probably lie very near the points of death. In contrast, the superabundant giraffids of bed 3aN probably died mainly by drowning during high floods, perhaps some distance from where the bones occur today, judging by the lack of articulated skeletons and the frequency of abrasion. In this paper the mortality profile analysis is extended to other QSM and PPM species, especially the alcelaphines of PPM beds 3aS and 3aN.

THE ELANDSFONTEIN FOSSIL SITE

Elandsfontein (= 'Saldanha' = 'Hopefield') (33°05'S 18°15'E) is located approximately 100 km north-north-west of Cape Town and roughly 10 km from Langebaanweg (Fig. 8). Covering an area of approximately 1,5 × 3 km, the site consists of a series of large barchan dunes separated by 'bays' in which deflation has exposed numerous mammalian fossils and occasional artefacts. Singer (1957) initiated scientific research, consisting mainly of surface collecting, at the site in 1951. Limited excavations were conducted in the early 1960s, most notably at the 'Cutting 10 Acheulean Site' (Singer & Wymer 1968; Klein 1978a). Except for occasional one-day status checks by staff of the South African Museum or the University of Stellenbosch, the site has been largely neglected since 1966. In 1981 G. and D. M. Avery of the South African Museum reinitiated scientific research at the site.

Most of the fossils found at Elandsfontein occur in or on a nodular calcareous duricrust that Butzer (1973) interprets as a subsoil manifestation of a former land-surface. It is possible that more than one such duricrust, and thus more than one former land-surface, are represented. Some fossils are also associated with a stratigraphically higher ferruginous duricrust, related to a somewhat more recent palaeo-surface. Finally, a small proportion of the fossils (including all those from the 'Bone Circle' of Inskip & Hendey 1966) have been found in loose sands above the ferruginous duricrust. Butzer believes the Elandsfontein geologic sequence reflects climatic oscillations between wetter and drier during a large portion of the Middle and Upper Pleistocene.

The Elandsfontein fauna comprises one or two species of tortoise (*Chelonia*), a small number of bird species (most prominently ostrich, *Struthio camelus*), and more than fifty species of mammals (Hendey 1974), including 'Saldanha Man' represented by a skull cap and a mandible fragment found on the surface in 1953 (Drennan 1953, 1955; Singer 1954, 1958; Rightmire 1976). Unfortunately, most of the bones that are presently available for study were collected from the surface without any record of their position within the site or of their fossil associations, so it is impossible now to relate them to each other or to the geology. Still, on taxonomic grounds, it is clear that there are at least two faunal stratigraphic units represented, a Middle Pleistocene one and an Upper Pleistocene one (Hendey 1974; Klein 1978a). Mid-Pleistocene fossils, probably including the 'Saldanha Skull', predominate heavily.

The Middle Pleistocene fossils were probably all associated with the calcareous duricrusts, while the Upper Pleistocene ones probably came from the ferruginous crust or from the overlying loose sands. In keeping with the possibility of multiple calcareous crusts, the taxonomic composition of the Middle Pleistocene fauna suggests it may be a composite of faunas spanning a large portion of the Middle Pleistocene, as this is now commonly defined (from the beginning of the Brunhes Normal Palaeomagnetic Epoch, approximately 700 000 years ago, to the beginning of the Last Interglacial, approximately 130 000 years ago).

Although the contexts of most of the Elandsfontein bones presently available for study were not recorded, it is probable that they occurred in basically the same contexts as the numerous bones that have been exposed by deflation at the site since 1966, when compilation of the collection essentially ceased. At the site today clusters of bones clearly gnawed by porcupines are common (as are porcupine-gnawed specimens in the collected sample). Perhaps equally frequent are semi-articulated portions of skeletons, particularly crania, vertebrae, ribs, and distal extremities of a giant buffalo (*Pelorovis* sp.), which is perhaps the most abundant mammalian species at the site. In both the already collected and presently exposed samples, stone artefacts are relatively rare, as are bones unquestionably cut or bashed by artefacts. Hyena coprolites, and bones exhibiting damage from carnivore teeth are probably more common. The overall impression is that the site is a complex aggregation of occurrences—porcupine burrows, 'natural' deaths, hyena burrows, and occasional hominid camps or kills—all now resting on the same deflation surfaces. Animals were probably drawn to the locality by the availability of perennial surface water throughout much, if not all, of the Middle and Upper Pleistocene.

The ungulate mortality profiles presented in this paper represent the first attempt to determine whether the available Elandsfontein collections can be made to provide palaeoecological information, in spite of the less-than-ideal way in which they were compiled and the obvious complexity of the site.

THE LANGEBAANWEG AND ELANDSFONTEIN UNGULATE SAMPLES AND AGE PROFILES

Table 3 lists the Langebaanweg and Elandsfontein ungulate taxa whose mortality profiles are considered here. In order to be included, a taxon had to be represented by a minimum of ten individuals that could be aged from teeth. Table 3 also presents the dental eruption and wear parameters (AGE_e, AGE_s, and AGE_{pel}) that were used to calculate individual ages from crown heights. The initial (unworn) crown heights (CH₀) used are presented in Table 4.

A complication in the Langebaanweg samples is that teeth cannot always be identified to species. Thus, while it is clear that two species of *Damalacra* are represented by horn-cores (Gentry 1980), the species cannot be readily separated even on complete dentitions. Similarly, although most of the teeth assigned to *Giraffa* sp. probably come from a single species, some probably derive from a dentally very similar species of palaeotragine, which is represented at Langebaanweg by occasional limb bones and ossicones (Hendey 1981a). Finally, although most of the *Nyanzachoerus* teeth probably come from a single species (*N. cf. pattersoni*), some (in the PPM) probably come from a dentally very similar second species (*N. cf. jaegeri*) (Hendey 1981a).

The choice was then either to exclude the *Damalacra*, *Giraffa* and *Nyanzachoerus* samples from consideration or to analyse them as if only one species were represented in each case. The second alternative was chosen, since it

TABLE 3

The ages of dental eruption (AGEe), shedding (AGEs), and potential ecological longevity (AGEpel) used to calculate age from crown height in the Langebaanweg and Elandsfontein ungulate samples considered in this paper. For extinct species, ages were inferred from published ages for closely related extant species. Where extinct species differed in size from their extant counterparts, the ages for the extinct species were adjusted by a factor reflecting the size difference. All quoted ages are in years.

Sources on pertinent ages in the extant species are: black rhinoceros (*Diceros bicornis*)—Goddard (1970); Burchell's zebra (*Equus burchelli*)—Klingel (1965), Klingel & Klingel (1966), Smuts (1974); mountain zebra (*Equus zebra*)—Joubert (1972); giraffe (*Giraffa camelopardalis*)—Hall-Martin (1976); bush-pig (*Potamochoerus porcus*)—Sowls & Phelps (1968); Cape buffalo (*Syncerus caffer*)—Grimsdell (1973), Sinclair (1977); greater kudu (*Tragelaphus strepsiceros*)—Simpson (1966); Lichtenstein's hartebeest (*Alcelaphus lichtensteini*)—Mitchell (1965); tsessebe (*Damaliscus lunatus*)—Huntley (1973); black wildebeest (*Connochaetes gnou*)—Von Richter (1971, 1974); eland (*Taurotragus oryx*)—Kerr & Roth (1970); and Cape grysbok (*Raphicerus melanotis*)—Manson (1974), and personal observation. Mentis (1972) was consulted for estimates of potential ecological longevity in all relevant extant species.

 LANGEBAANWEG

	dP $\bar{4}$		P $\bar{4}$		
	AGEe	AGEs	AGEe	AGEpel	Source
<i>Cerathotherium praecox</i>	0	6	6	35	Inference from dentally very similar black rhinoceros.
	dP $\bar{2}$		P $\bar{2}$		
	AGEe	AGEs	AGEe	AGEpel	
<i>Hipparion cf. baardi</i>	0	3	3	20	Assumption that <i>H. cf. baardi</i> parameters would be roughly 10% smaller than those for Burchell's zebra and mountain zebra.
	dP $\bar{4}$		M $\bar{3}$		
	AGEe	AGEs	AGEe	AGEpel	
<i>Giraffa sp.</i>	0	4,5	3,5	28	Inference from dentally very similar modern giraffe.
<i>Sivatherium hendeyi</i>	0	6	4,67	37,24	Assumption that <i>S. hendeyi</i> parameters would be roughly 33% larger than those of modern giraffe.
<i>Mesembriportax acrae</i>	0	2,5	2	18	Inference from extant bovids of similar size, such as greater kudu, Lichtenstein's hartebeest, and black wildebeest.
<i>Simatherium demissum</i>	0	3,0	2,5	20	Assumption that <i>S. demissum</i> parameters would be roughly 25% smaller than those of Cape buffalo.
<i>Damalacra spp.</i>	0	2,5	2	18	Inference from extant bovids of similar size, such as greater kudu, Lichtenstein's hartebeest, tsessebe, and black wildebeest.
<i>Nyanzachoerus sp(p).</i>	0	2,5	2	18	Assumption that <i>Nyanzachoerus</i> parameters would be roughly 20% greater than those for bush-pig.

ELANDSFONTEIN					
	dP $\bar{2}$		M $\bar{3}$		
	AGEe	AGEs	AGEe	AGEpel	Source
<i>Equus capensis</i> .	0	3,6	3,6	26,4	Assumption that <i>E. capensis</i> parameters would be roughly 20% larger than those for Burchell's zebra and mountain zebra.
	dP $\bar{4}$		M $\bar{3}$		
	AGEe	AGEs	AGEe	AGEpel	
<i>Pelorovis</i> sp.	0	4,35	3,28	26,4	Assumption that <i>Pelorovis</i> parameters would be roughly 10% greater than those for Cape buffalo.
<i>Taurotragus oryx</i>	0	3,6	2,5	20	Data on modern eland.
<i>Hippotragus gigas</i>	0	4	3	24	Assumption that <i>H. gigas</i> parameters would be similar to those of Cape buffalo.
	dP $\bar{4}$		M $\bar{1}$		
	AGEe	AGEs	AGEe	AGEpel	
<i>Raphicerus</i> sp.	0	1,25	0,25	6	Inference from closely related Cape grysbok.

seemed unlikely that mixed samples would produce interpretable age profiles unless one member of a pair heavily dominated a sample or both members were, in fact, characterized by the same profile shape to begin with.

In order to obtain a complete age (mortality) profile for each taxon, it was necessary to make crown height measurements on a deciduous tooth and on a permanent one that erupted before the deciduous tooth was shed. For each taxon, the choice of an appropriate deciduous-permanent pair was determined by:

- (i) the abundance of various teeth (probably dictated mainly by relative durability; for example, in most species, mandibular teeth are more durable than maxillary ones, and molars are more durable than premolars);
- (ii) the extent to which it was possible to determine the former place in the mouth of an isolated tooth (for example, in most species, isolated M1's are difficult to tell from M2's from the same jaw, while isolated M3's are immediately recognizable);
- (iii) the ease of measurement (particularly important in the case of a species represented by a number of teeth still mounted in jaws; in such an instance the base of the crown of a late-erupted tooth (e.g. M3) will often be masked by jaw-bone, and crown height can be measured only on a tooth (e.g. M1) that entered occlusion considerably earlier).

The crown heights and age profiles (calculated by the linear formulae) for Langebaanweg *Sivatherium hendeyi* (bed 3aN), *Giraffa* sp. (and palaeotragine) (bed 3aN), *Ceratotherium praecox* (QSM), *Mesembriportax acrae* (QSM and bed 3aN), and *Simatherium demissum* (bed 3aN) were presented in an earlier paper (Klein 1981a). The age profiles alone, recalculated using the quadratic

TABLE 4

The initial (unworn) crown heights (in mm) used to calculate the age profiles of the Langebaanweg and Elandsfontein ungulate species considered in this paper.

	$d\bar{P}_4$	\bar{P}_4
<i>Ceratotherium praecox</i>	45,0	65,1
	$d\bar{P}_2$	\bar{P}_2
<i>Hipparion</i> cf. <i>baardi</i>	25,0	60,0
	$d\bar{P}_2$	\bar{M}_3
<i>Equus capensis</i>	30,0	90,0
	$d\bar{P}_4$	\bar{M}_1
<i>Raphicerus</i> sp.	5,4	10,6
	$d\bar{P}_4$	\bar{M}_3
<i>Giraffa</i> sp.	16,3	27,8
<i>Sivatherium hendeyi</i>	23,4	45,1
<i>Nyanzachoerus</i> sp(p).	—*	45,1
<i>Damalacra</i> spp.	15,0	39,6
<i>Mesembriportax acrae</i>	10,0	33,0
<i>Simatherium demissum</i>	16,3	36,0
<i>Pelorovis</i> sp.	22,7	71,5
<i>Hippotragus gigas</i>	23,9	54,7
<i>Taurotragus oryx</i>	19,0	44,8

* No specimens

formulae, are presented here in Figure 15. The crown heights and age profiles (calculated by the quadratic formulae) for Langebaanweg *Damalacra* spp. (beds 3aS and 3aN), *Nyanzachoerus* sp(p). (QSM and PPM) and *Hipparion* cf. *baardi* (QSM and PPM), and for Elandsfontein *Equus capensis*, *Hippotragus gigas*, *Taurotragus oryx*, *Raphicerus* sp., and *Pelorovis* sp. are presented here in Figure 7 and Figures 9–13. Figure 14 presents a recasting of the Langebaanweg *C. praecox* crown heights and age profile, based on a somewhat larger sample than in the earlier paper (and with the age profile calculated by the quadratic formulae).

The various Figures also illustrate the crown height dimension that was measured in each case. In general, this dimension was the minimum distance between the occlusal surface of a tooth and the line separating the enamel of the crown from the dentine of the roots, measured on the buccal surface of mandibular teeth and on the lingual surface of maxillary ones. On multilobed (or multilophed) teeth the measurement was made on the first (anteriormost) lobe (or loph), except in samples specifically noted in the Figures, where it was necessary to measure the second lobe because the first one was so often damaged or missing.

Finally, the Figures present and illustrate crown breadth measurements for each taxon. These were analysed for excessive variability and for deviations from statistical normality that may indicate the underlying samples were mixed or heterogeneous. In no instance was a significant departure from normality detectable. This is a particularly important finding in the case of these dental samples—especially the large one of *Damalacra* from Langebaanweg—that probably or certainly derive from two closely related species. If the crown

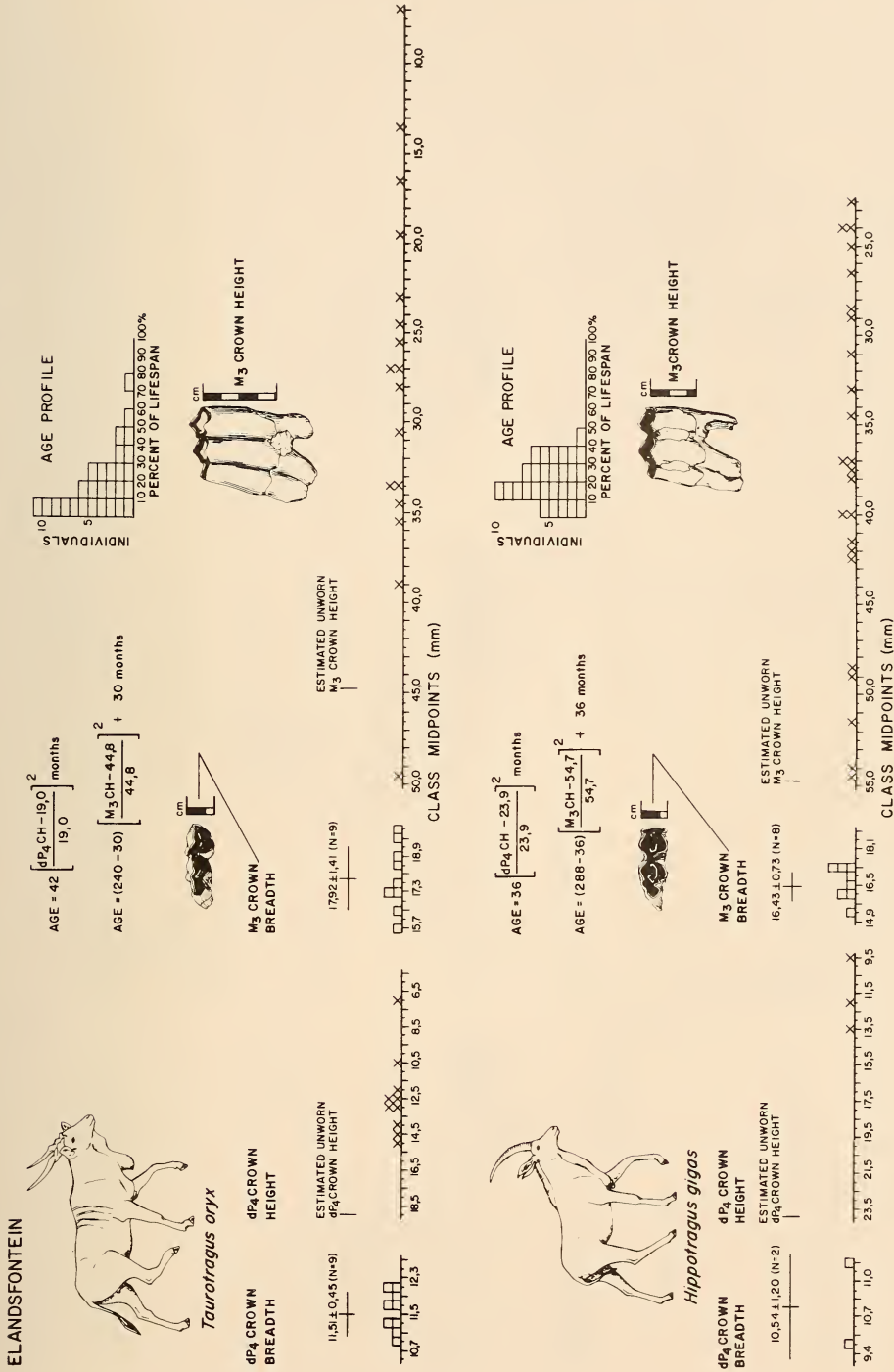


Fig. 9. dP_4 and M_3 crown breadths and crown heights of *Taurotragus oryx* and *Hippotragus gigas* from Elandsfontein, and the age (mortality) profiles calculated from the crown heights.

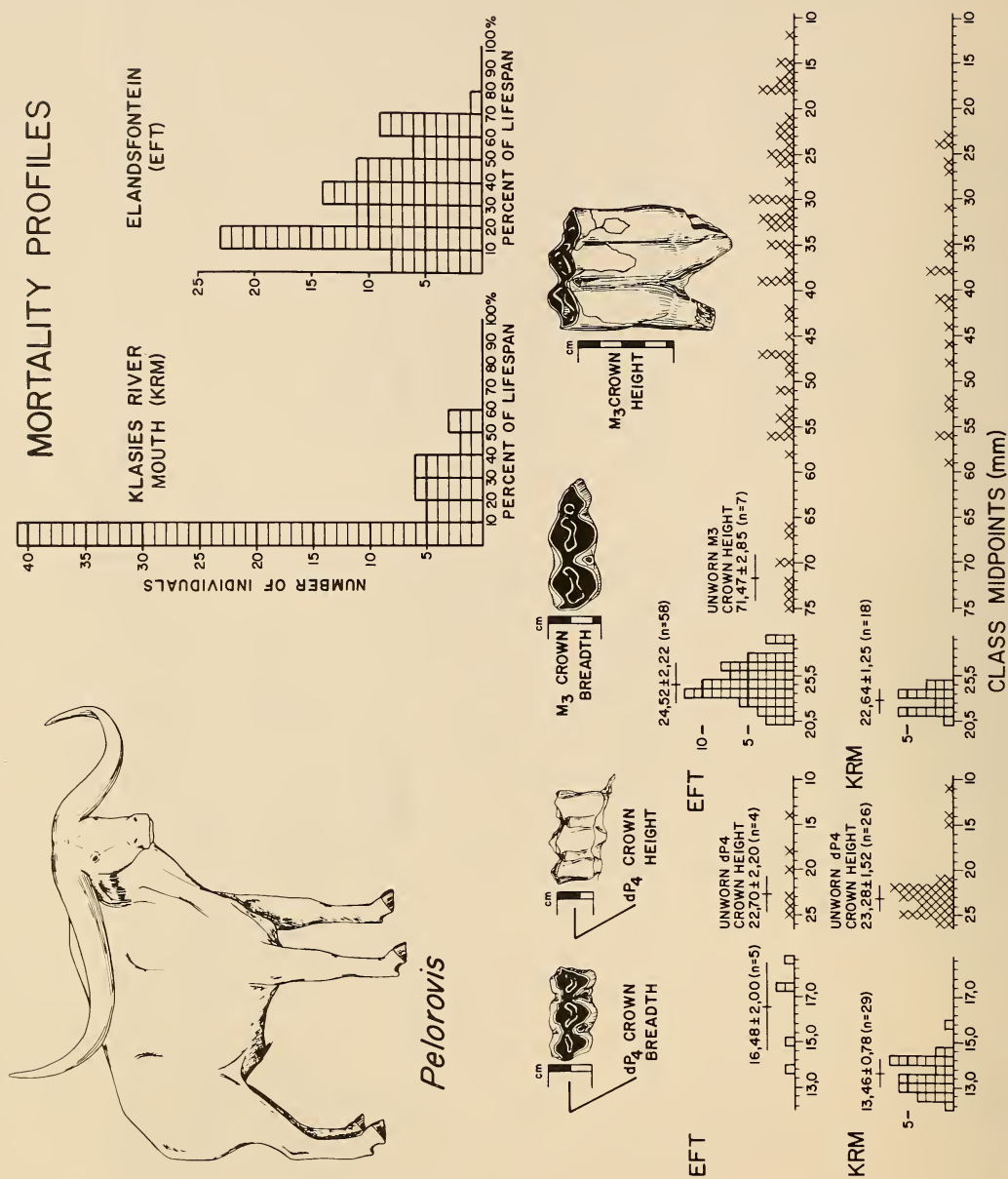
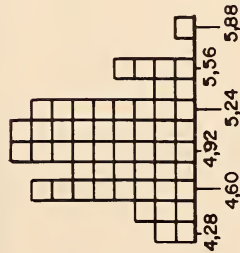


Fig. 10. dP₄ and M₃ crown breadths and crown heights of *Pelorovis* from Elandsfontein and Klasies River Mouth Cave 1, and the age (mortality) profiles calculated from the crown heights. The much greater abundance of very young individuals (in the first 10% of lifespan) in the Klasies River profile suggests that the Klasies River Stone Age people actively hunted *Pelorovis*, for reasons discussed in the text.

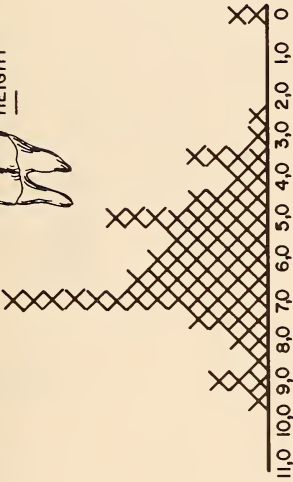
ELANDSFONTEIN



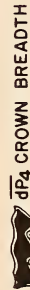
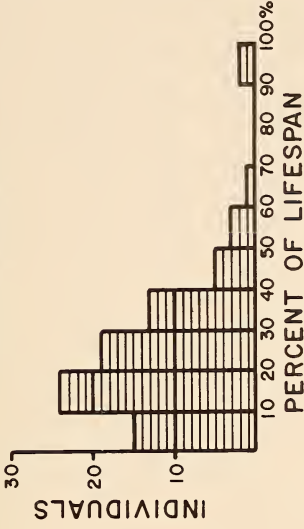
$49,50 \pm 3,46$ (N=52)



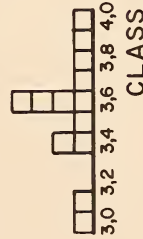
ESTIMATED UNWORN M_1 CROWN HEIGHT



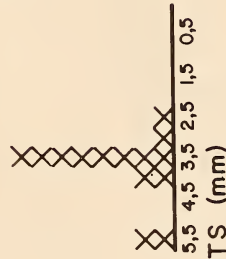
AGE PROFILE



$35,54 \pm 2,85$ (N=13)



ESTIMATED UNWORN dP_4 CROWN HEIGHT



Raphicerus sp.

Fig. 11. dP_4 and M_1 crown breadths and crown heights of *Raphicerus* sp. from Elandsfontein, and the age (mortality) profile calculated from the crown heights.

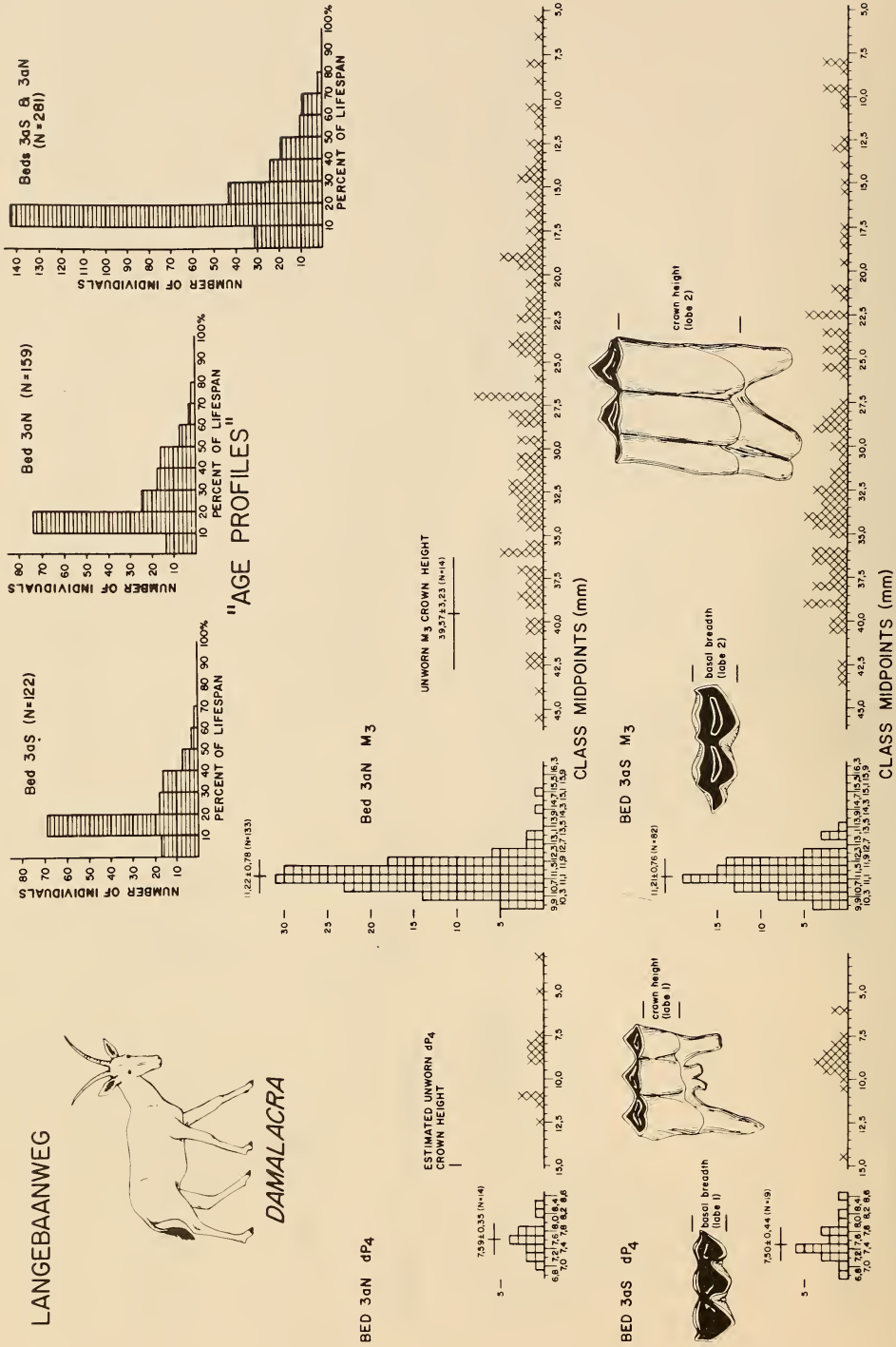
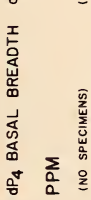
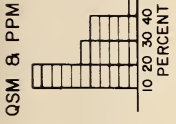
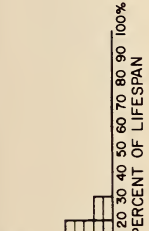
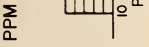
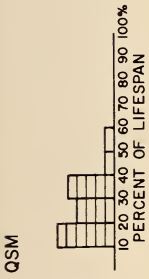
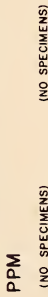


Fig. 12. dP₄ and M₃ crown breadths and crown heights of *Damalacra* spp. from Beds 3aS and 3aN at Langebaanweg, and the age (mortality) profiles calculated from the crown heights.

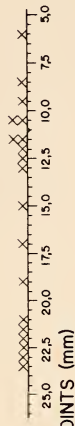
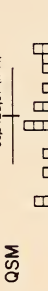
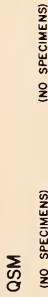
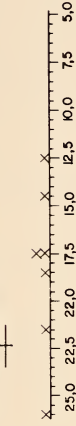
'AGE PROFILES'



dP4 CROWN HEIGHT

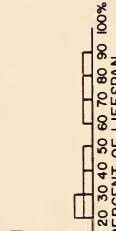


UNWORN M3 CROWN HEIGHT
22.5 ± 1.03 (N=5)

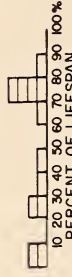


QSM

PPM



QSM & PPM



dP2 CROWN HEIGHT

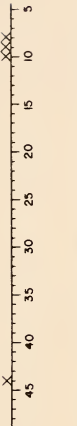
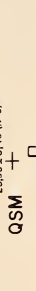
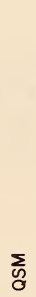
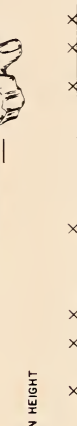
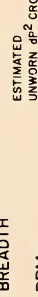
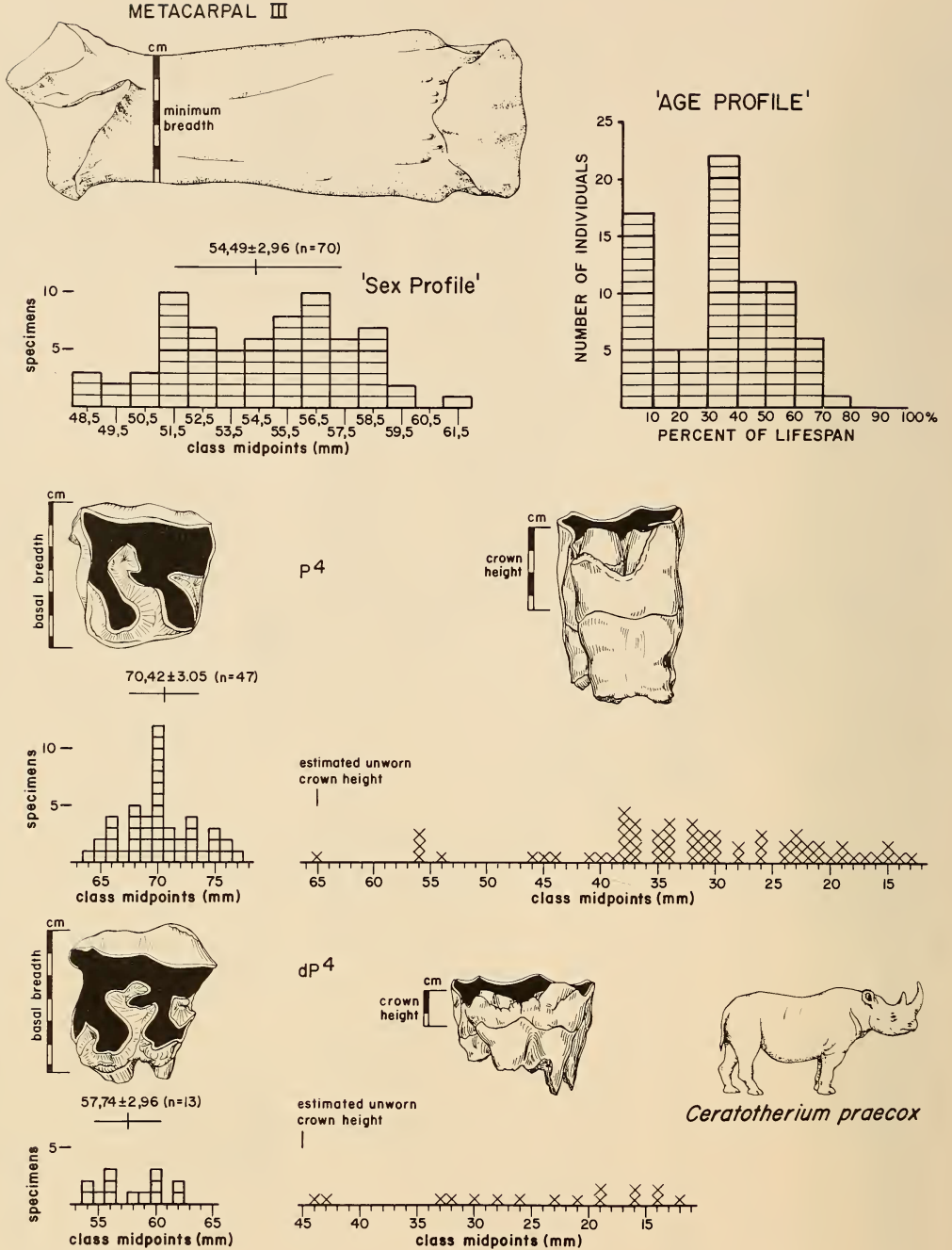


Fig. 13. Above: dP4 and M3 crown breadths and crown heights of *Nyanzachoerus* from Langebaanweg, and the age (mortality) profiles calculated from the crown heights. Below: dP2 and p2 crown breadths and crown heights of *Hipparion* from Langebaanweg, and the age (mortality) profiles calculated from the crown heights.



LANGEBAANWEG

Fig. 14. Below: dP $\bar{4}$ and P $\bar{4}$ crown heights and crown breadths of *Ceratotherium praecox* from Langebaanweg. Above right: the age (mortality) profile calculated from the crown heights. Above left: the distribution of measurements of the minimum mediolateral diameter ('minimum breadth') of the third metacarpal of *Ceratotherium praecox* from Langebaanweg. The two modes probably represent the sexes, as discussed in the text.

breadth distribution had departed significantly from normality, then the use of a single set of constants to calculate ages from crown heights in the mixed samples would be open to serious question.

All crown heights and breadths were measured to the nearest tenth of a millimetre with a single pair of Helios dial-reading calipers.

INTERPRETATION OF THE LANGEBAANWEG AND ELANDSFONTEIN AGE PROFILES

Figure 15 presents the Langebaanweg and Elandsfontein age profiles in directly comparable summary form. With the exception of females in *Nyanzachoerus* (Langebaanweg) and *Raphicerus* (Elandsfontein), females in all the taxa involved probably had no more than one young per year, based on observations of their living representatives or of their closest living relatives. With the exceptions of *Nyanzachoerus* and *Raphicerus* then, all the taxa were probably characterized by catastrophic ('lx') and attritional ('dx') profiles that were very different in form. More specifically, each species would have a catastrophic profile in which successively older age classes contained progressively fewer individuals. It would have an attritional age profile that was either U-shaped, with a large mode in the youngest class and a second smaller one in an age class beyond 40 per cent of potential lifespan, or possibly L-shaped, with a large mode in the youngest age class and no obvious modes thereafter.

From Figure 15, it is apparent that the relevant profiles do separate fairly clearly between the expected attritional and catastrophic types. Thus, the profiles for Langebaanweg *Ceratotherium praecox* (QSM), *Mesembriportax acrae* (QSM), *Simatherium demissum* (bed 3aN), and *Hipparion* cf. *baardi* (QSM and PPM composite) are all basically attritional, while those for Langebaanweg *Sivatherium hendeyi* (bed 3aN), *Giraffa* sp. (bed 3aN), and *Damalacra* spp. (beds 3aS and 3aN), and for Elandsfontein *Equus capensis*, *Hippotragus gigas*, and *Taurotragus oryx* are all basically catastrophic.

A problem arises with respect to the profiles of Langebaanweg *Mesembriportax acrae* (PPM 3aN) and Elandsfontein *Pelorovis* sp., which could be interpreted as either catastrophic or L-shaped attritional. Since the *Pelorovis* profile is based on a relatively large sample and since its form contrasts with the clearly catastrophic form of the profile for *Equus capensis*, based on a sample of similar size, it seems most likely that the *Pelorovis* profile is attritional or perhaps mixed attritional-catastrophic. There is also a problem with regard to the Langebaanweg *Hipparion* cf. *baardi* profile, which contains enough individuals for consideration only when material from two very different sedimentary units is lumped. Although its form appears clearly attritional, it will be ignored in what follows.

The profiles that appear to be clearly attritional are not completely identical to each other, nor are those that appear to be clearly catastrophic. Some of the differences are probably due to chance ('sampling error'), particu-

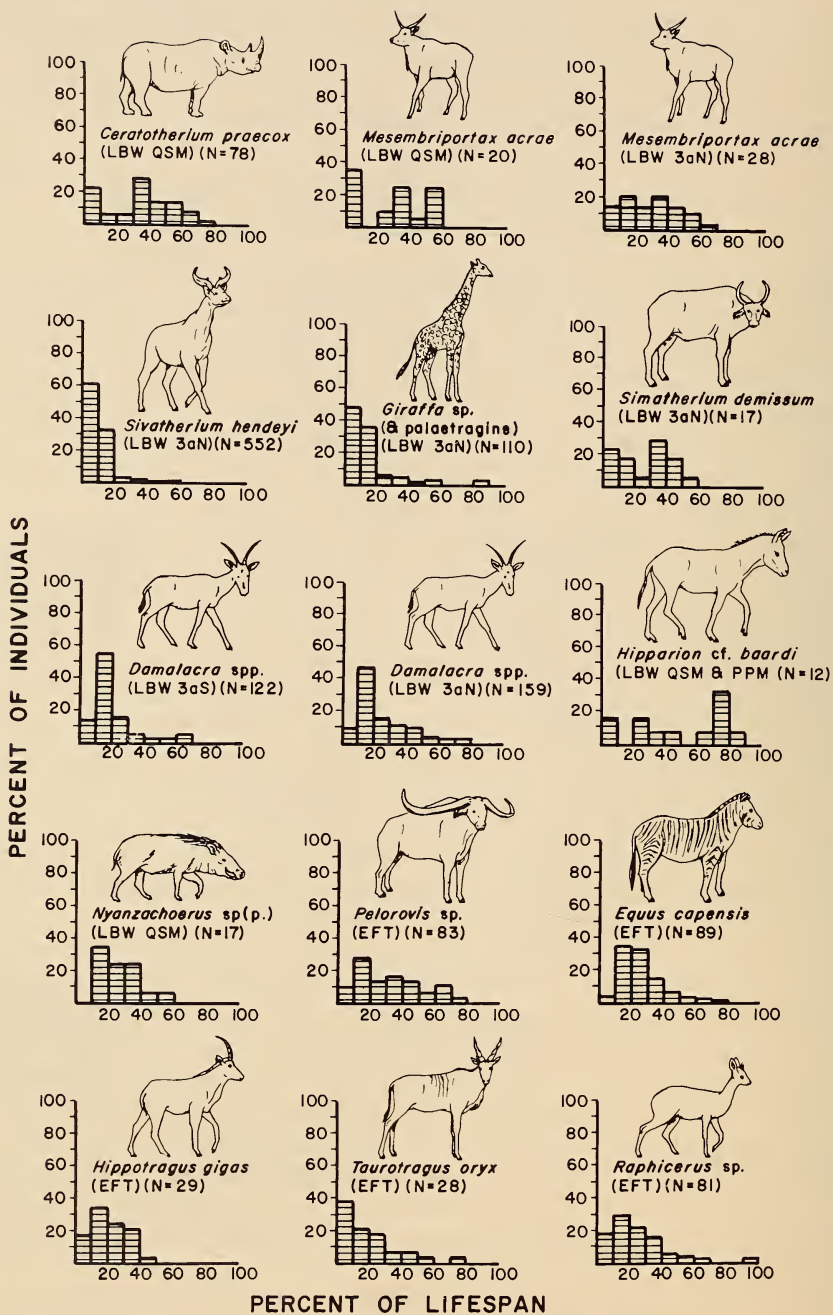


Fig. 15. Age (mortality) profiles of all the Langebaanweg and Elandsfontein ungulate species discussed in the text.

larly likely to affect some of the smaller samples. Other differences are probably due to errors in the constants used in the age estimation formulae. Such errors are almost certainly too small to affect overall profile shape, but could well affect the precise content of particular age classes.

Neither chance nor the constants used in the formulae, however, can explain the fact that all the profiles except the ones for *Sivatherium hendeyi* and *Giraffa* sp. (and palaeotragine) contain many fewer very young individuals (in the first 10% of lifespan) than would be expected in either a catastrophic or an attritional age profile. At both Langebaanweg and Elandsfontein bone preservation is good to excellent, so that selective post-depositional destruction of very young (relatively fragile) jaws and teeth is probably not the reason for their frequent underrepresentation. Much more likely is pre-depositional destruction or removal, primarily by scavengers.

It was pointed out above that selective destruction or removal of the bones of very young individuals almost certainly accounts for their underrepresentation in mortality profiles based on jaws collected recently by wildlife biologists. The smaller the species, the greater the underrepresentation, which probably accounts for the fact that very young individuals are so poorly represented in *Damalacra* spp. as against their abundance in the giraffids, though in both cases, the basic mortality pattern is catastrophic. In order to avoid confrontations with other scavengers attracted to catastrophic death sites, individual scavengers probably often carried off the carcasses of very young *Damalacra*, but had to feed in place on the much larger (and relatively less fragile) carcasses of very young giraffids.

The catastrophic age profiles for *Sivatherium*, *Giraffa*, and *Damalacra* from the Langebaanweg PPM (beds 3aS and 3aN) suggest that death occurred by drowning during peak or flash flooding. This suggests in turn that *Damalacra* and the giraffids are so much more abundant than other species in the PPM channel fills because their feeding habits tied them to the ancient river even during those periods (?seasons) when increased precipitation meant that surface water and green vegetation were widespread. For the giraffids, the river margins might have been fatally attractive because the trees or high bush on which they fed were restricted to this environment. For *Damalacra* spp. the attraction might have been floodplain meadows or the ecotone between riverine forest and fringing grassland, habitats clearly favoured today by their close living relative the tsessebe (*Damaliscus lunatus*) (Smithers 1971; Child *et al.* 1972).

Hendey (1981a) has suggested that between the deposition of bed 3aS (earlier) and bed 3aN (later), grassland increased at the expense of bush and forest in the ancient Langebaanweg environment. By 3aN times bush and forest might have been all but absent away from the river margins. This could account for the remarkable increase in giraffids compared to *Damalacra* in the bed 3aN (compared to 3aS) channel fill. The nutritional stress that habitat reduction induced in the bed 3aN sivatheres may explain the hypoplasia that is sometimes obvious in their dental enamel (Hendey 1981a).

The attritional profiles of *Ceratotherium praecox* and *Mesembriportax acrae* from the Langebaanweg QSM suggest that death occurred mainly as a result of predation, disease, starvation and other attritional factors, in keeping with a mode of bone occurrence and sedimentary context that imply subaerial death very near the places where the bones lie. The attritional profiles of *Simatherium demissum* and possibly of *Mesembriportax acrae* from the Langebaanweg PPM channel fills are more difficult to understand. Given the rarity of these species in the PPM, it is possible their bones were either swept by the river from the adjacent floodplain or reworked from deposits of a more ancient floodplain on which attritional mortality was the rule. It is further possible that the ambiguous, neither clearly catastrophic nor clearly attritional, shape of the PPM 3aN *M. acrae* profile reflects a mixture of catastrophic mortality by drowning and attritional mortality on the adjacent floodplain.

The probably attritional shape of the *Pelorovis* age profile from Elandsfontein is in keeping with the fact that this species is commonly represented by semi-articulated skeletons scattered across the ancient land-surface(s) now exposed by deflation at the site. It is not difficult to imagine that *Pelorovis* deaths were due mainly to attritional factors at or near the ancient waterholes that probably led to concentrations of animals at Elandsfontein.

Whatever the precise causes of *Pelorovis* mortality at Elandsfontein, the rarity of very young individuals is interesting in so far as these are well represented in an attritional profile of *Pelorovis* from the Middle Stone Age (early Upper Pleistocene) archaeological site of Klasies River Mouth (Klein 1978b) (Fig. 10 here). Since the rarity of very young *Pelorovis* at Elandsfontein probably reflects pre-depositional destruction or removal by carnivores and scavengers, their abundance in an archaeological site implies either that people were able to locate the carcasses of very young individuals before other predators or that they actively hunted the very young. A priori, the second alternative seems more likely.

With the *Pelorovis* profile in mind, it is puzzling that the other relatively abundant large ungulates at the site—*Equus capensis*, *Hippotragus gigas*, and *Taurotragus oryx*—are characterized by catastrophic rather than attritional profiles. In the case of *H. gigas* and *T. oryx* it is possible that larger samples would turn what now appear to be catastrophic profiles into L-shaped attritional ones, but the *Equus capensis* sample is clearly too large to suppose that even a substantial increase in size would transform what is an almost classic catastrophic profile into an attritional one.

At Elandsfontein today, the bones of *Equus capensis* (and of most other species) appear to occur differently than do *Pelorovis* bones, with fewer instances of semi-articulated skeletons. This may reflect the fact that *E. capensis* (and most other species) lacked the massive skulls and vertebral columns of *Pelorovis* sp., so that semi-articulated *E. capensis* skeletons are both less likely to occur and less likely to be noticed, or it may mean that the *E. capensis* bones are coming mainly from deflated porcupine or carnivore lairs.

An indeterminate, albeit smaller, proportion of the *Pelorovis* bones may also come from such lairs, adding a pseudo-catastrophic overlay to an otherwise essentially attritional profile. Skeletal element counts from the fossil carnivore (probable hyena) lairs at Swartklip and elsewhere in southern Africa show size or weight sorting of large ungulate bones that may bias age profiles based only on teeth towards the catastrophic side (Klein 1975, and unpublished).

As a final alternative, it is possible that the *E. capensis* bones derive mainly from predation by a creature that had the ability to kill individuals of all ages in roughly their live proportions. Further speculation on this would be fruitless, and perhaps the major point to be made is that the interpretative potential of mortality profile analysis is obviously dependent upon the availability of good contextual information.

With respect to the *Nyanzachoerus* profile (Langebaanweg QSM) and the *Raphicerus* profile (Elandsfontein), sample profile shape alone is inadequate for determining whether death was largely attritional or catastrophic. This is because female *Nyanzachoerus* probably had litters of two or more, as have extant African suids (Mentis 1972). Extant *Raphicerus* females generally bear just one young at a time, but are fully capable of producing two surviving young per year (Mentis 1972). Given this reproductive potential, high rates of mortality in the fossil populations of *Nyanzachoerus* and *Raphicerus* could well have continued into young adult age classes, leading to catastrophic and attritional profiles that would both have the down-staircase form of catastrophic mortality in a species where females have a much lower reproductive rate.

Figure 15 shows that the *Nyanzachoerus* and *Raphicerus* profiles both exhibit down-staircase shapes. Since the *Nyanzachoerus* material was drawn from a sedimentary unit (Langebaanweg QSM) in which context and the mortality profiles of other species imply that attritional mortality was the rule, it seems most likely that the *Nyanzachoerus* profile, in fact, reflects attritional mortality in a species that regularly bore two young or more at a time.

It is more difficult to argue that attritional mortality is probably reflected in the Elandsfontein *Raphicerus* profile, because it is unclear from modern observations whether female *Raphicerus* do commonly produce two young per year. The problem is that *Raphicerus* spp. (grysbok and steenbok) are solitary, secretive, and inconspicuous, in short, difficult to observe systematically. It is pertinent, however, that *Raphicerus* mortality profiles from a wide variety of southern African sites, including both archaeological ones (Die Kelders, Nelson Bay, Klasies River Mouth, and others) and carnivore (probable hyena) ones (Swartklip, Sea Harvest, and others), all display the same down-staircase shape as the Elandsfontein profile (Klein 1981b) (Fig. 16 here). None of the profiles displays the classic U- or L-shape that would reflect attritional mortality in a species characterized by a birth rate of one young (or less) per female per year.

The essential similarity in form of the *Raphicerus* profiles from such a wide variety of contexts, where both attritional and catastrophic mortality are probably represented, strongly suggests that *Raphicerus* populations are,

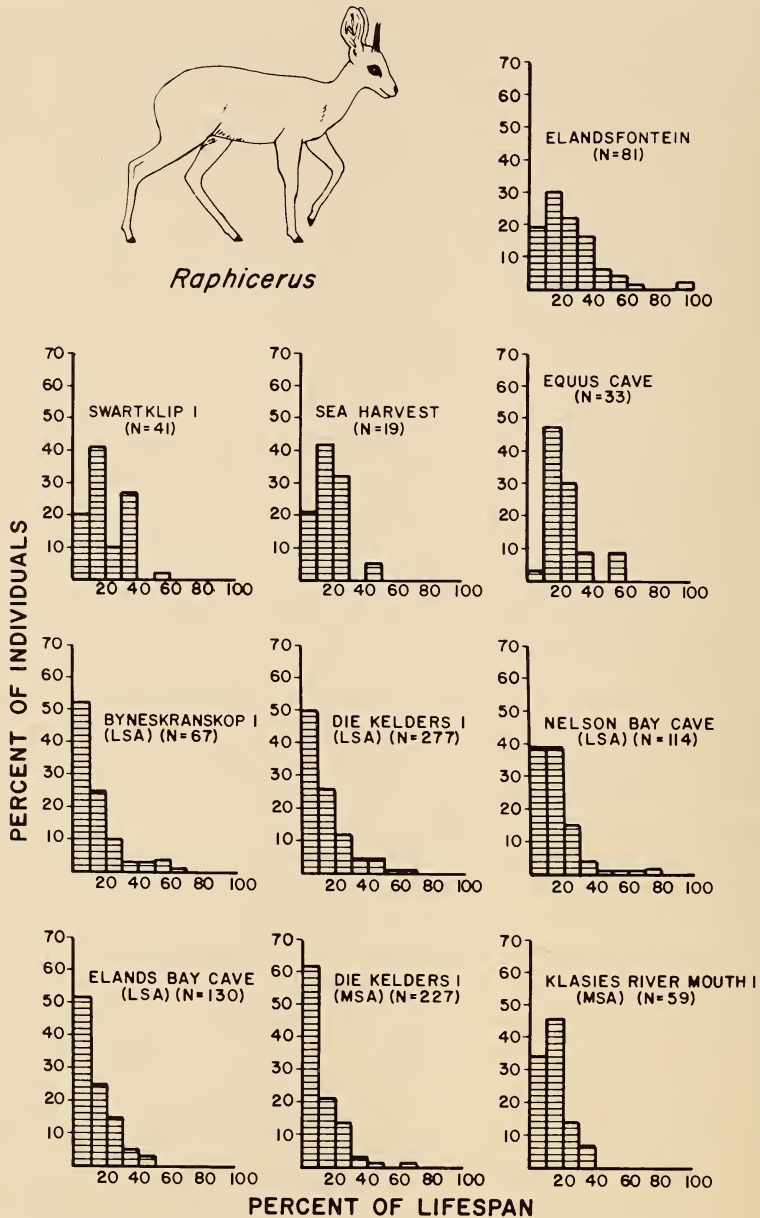


Fig. 16. Age (mortality) profiles of *Raphicerus* from Elandsfontein and from the fossil carnivore (probable hyena) lairs at Swartklip, Sea Harvest, and Equus Cave, the Middle Stone Age levels of Die Kelders Cave 1 and Klasies River Mouth Cave 1, and the Late Stone Age levels of Byneskranskop Cave 1, Nelson Bay Cave, Elands Bay Cave, and Die Kelders Cave 1. Very young individuals are probably underrepresented in several of the profiles because of the relative fragility of their jaws and teeth. Keeping this fact in mind, the profiles all display a general tendency for successively older age classes to contain progressively fewer individuals. Since some (?most) of the profiles are probably attritional, while others may be catastrophic, the implication is that *Raphicerus* females commonly bear more than one young per year, as discussed in the text.

indeed, ones in which catastrophic and attritional profiles do not contrast notably in form. This would be the case only if female *Raphicerus* regularly produce two young per year. The *Raphicerus* example points up the fact that age profiles based on fossil samples may be used to draw basic biological inferences—in this case, the common rate of reproduction—that may be difficult to determine from observations of live populations.

SEASON OF BONE ACCUMULATION AT LANGEBAANWEG AND ELANDSFONTEIN

It was pointed out above that individuals from a fossil population in which both birth and death were seasonally restricted events would fall into discrete age classes or clusters, each separated from the next by an age gap in which no individuals occur. Kurtén (1953) was probably the first to point out that crown heights of a tooth drawn from a population with a discontinuous age distribution may also form clusters or modes, each cluster representing a group of individuals born at about the same time. In his study of the same north Chinese ungulates discussed above (age profiles in Figure 5), he believed he could detect crown height modes reflecting seasonal birth or death, the latter probably by flooding (drowning).

In his study of the extinct pronghorn antelope, *Merycodus furcatus*, Voorhies (1969) also found crown height multimodality. It is more convincing than in Kurtén's samples, since Voorhies's sample was so much larger. Variably convincing crown height multimodality, taken as evidence for seasonal birth and death, has also been reported for *Bison* spp. from several archaeological sites in the western United States (Frison 1978*b*, with references).

Both the crown height distributions and the distributions of estimated individual ages (ungrouped) of all the ungulate samples reported here were examined for multimodality that would reflect seasonal birth and death. The possibility of finding such multimodality seemed particularly good for the giraffids and *Damalacra* spp. from the Langebaanweg PPM channel fills, both because the flooding that was the probable cause of death might well have been seasonal and because the dental samples involved are quite large. However, a convincing pattern of multimodality was not found.

For the giraffids, the problem may be that, like their close living relative, *Giraffa camelopardalis* (Mentis 1972; Foster & Dagg 1972), they bore their young more or less throughout the year, without clear seasonal peaks. Additionally, giraffid teeth are low crowned relative to potential individual lifespan, so that crown height modes, even if they existed, would be very close together and difficult to detect, except in truly enormous samples. In this context it is pertinent that Klein *et al.* (1981) failed to find convincing crown height multimodality in a large sample of wapiti with a similarly low crown height to lifespan ratio, though seasonal birth and death in the wapiti population was historically documented.

It is also possible that *Damalacra* spp. were not seasonal breeders, though their closest living relatives, various alcelaphine antelopes, generally are (Mentis 1972). Furthermore, individuals of *Damalacra* spp. had much higher crowns and shorter potential lifespans than the giraffids. Perhaps the reason the *Damalacra* samples fail to exhibit clear multimodality is that they comprise two species, each with a somewhat different birth season or perhaps somewhat different initial crown heights and eruption schedules.

In sum, it remains possible that bones did accumulate in the Langebaanweg PPM channel fills seasonally, but it will take either larger samples, or more homogeneous ones, or both to show this from crown heights.

SEX RATIOS IN THE FOSSIL SAMPLES

Although ungulate species usually exhibit sexual dimorphism in bone morphology or size, or both, there are serious practical obstacles to estimating the sex ratio in most fossil samples. The principal problem is that the skeletal parts that reflect sex the best are generally not very durable, and they are often less durable in one sex than in the other. In bovids, for example, the skeletal part from which sex can be most readily determined is the frontlet or part of the skull that bears the horns. In most species female frontlets either lack horns or exhibit ones that are quite different in size or shape from male horns. The problem is that frontlets are among the least durable parts of the skeleton, and the pre- and post-depositional destructive pressures that have affected most fossil samples remove frontlets selectively. Thus in most samples they are too rare for the reliable estimation of a sex ratio. Additionally, male frontlets tend to be more robust than female ones, so that even when the number of frontlets is large enough to estimate a sex ratio, there is a likely bias in favour of males.

In the present context the relative fragility of frontlets, particularly female ones, almost certainly accounts for the fact that frontlets are much less common than other bovid skeletal elements (particularly jaws and teeth) at both Langebaanweg and Elandsfontein, while male frontlets clearly predominate.

In equids the skeletal parts from which sex can be most readily determined are the anterior portions of the jaws, which usually bear large canines in males and very small ('vestigial') canines or none in females. Unfortunately, the relevant parts of equid jaws are not very durable, while in females they are even less durable due to the lack of large canines. Again, in the fossil equid samples considered here, the relevant parts of the jaws are relatively rare and male specimens dominate heavily.

An alternative and, in general, less biased way to estimate the sex ratio derives from the fact that in most species, probably including all those considered here, bones of males are larger on average than their homologues in females (Boessneck & Von den Driesch 1978, with references). The search for size bimodality reflecting sex must generally be limited to bones on which the epiphyses are fused, or modes reflecting the sexes may be confounded with

ones reflecting different age groups. In any case, bones on which the epiphyses are unfused tend to be rare in many fossil samples, probably because of their relative fragility. In general, among bones with fused epiphyses, the most fruitful ones to scrutinize for size bimodality are those that bear weight, since they will probably reflect larger male size most strongly.

With regard to the samples considered here, three—those of *Ceratotherium praecox* from Langebaanweg and of *Equus capensis* and *Pelorovis* sp. from Elandsfontein—contain a sufficient number of mature, weight-bearing bones to undertake a search for size bimodality. In each case the most suitable bones in terms of sample size and the likelihood of showing a sex difference were the central metapodials (III or III/IV). (The numbers of central metacarpals and metatarsals were respectively 80 and 65 for *C. praecox*, 76 and 87 for *E. capensis*, and 127 and 96 for *Pelorovis* sp.) In so far as bone completeness permitted, a total of six measurements was made on each metapodial (maximum total length, maximum proximal mediolateral diameter, maximum proximal anteroposterior diameter, maximum distal mediolateral diameter, maximum distal anteroposterior diameter, and minimum mediolateral shaft diameter).

The measurements on both the metacarpals and metatarsals in each sample were examined for size bimodality, using the histogram-creating capability of IDA (Interactive Data Analysis—Ling & Roberts 1982), as implemented on the University of Chicago's Amdahl 470 computer. The advantage of using IDA is not only the speed with which it produces histograms from measurements but its ability to produce a histogram based on any desired class breadth or distribution midpoint. Sometimes a narrower class breadth, chosen second, will reveal bimodality that a broader one, chosen first, had masked.

No histogram of *Equus capensis* metacarpal or metatarsal measurements displayed convincing bimodality, while the only *Pelorovis* histogram to display any was that for total length of the metacarpal, and even in this case the bimodality was relatively weak. The problem is probably not that the sexes in *E. capensis* or *Pelorovis* sp. were the same in average size but rather that the difference in average size would show up clearly only in much larger metapodial samples.

The results for *Ceratotherium praecox* were more gratifying, in that a plot of the minimum mediolateral shaft diameter of metacarpal III showed clear and convincing bimodality, as reproduced here in Figure 14. Assuming the individuals represented by the lower mode of the plot are females and those represented by the higher mode are males, the plot suggests that male and female *C. praecox* are about equally represented. This compares with apparent parity in the adult sex ratios of the closest living relatives of *C. praecox*, the white rhinoceros (*C. simum*), and the black rhinoceros (*Diceros bicornis*) (Mentis 1972). The implication is that the pattern of attritional mortality reflected in the *C. praecox* age structure did not differ significantly between the sexes, as it apparently does not in the living relatives of *C. praecox*.

In sum, a reliable sex ratio is much more difficult to establish than a reliable age profile from fossil material. An additional complication, which should be noted here, is that even given a reliable sex ratio from a fossil sample, interpretation may prove difficult. This is because modern observations indicate that the sex ratio in ungulates varies considerably, both among species and among populations of the same species.

CONCLUSIONS

The principal conclusions of this paper may be listed as follows:

1. An ungulate species in which females regularly produce one young (or less) per year will have a catastrophic (= 'lx') age profile with a down-staircase shape in which successively older age classes contain progressively fewer individuals. The corresponding attritional (= 'dx') profile will tend to be U-shaped, with a large peak in the youngest age class and a second smaller peak beyond 40–50 per cent of potential individual lifespan, or L-shaped, with a large peak in the youngest age class and no obvious peaks thereafter.

2. An ungulate species in which females regularly produce more than one young per year will have catastrophic and attritional mortality profiles that both exhibit the down-staircase form. In such species, a difference in form between the profiles will occur mainly at the 'tail' of old individuals, which will tend to exhibit a small rise (or peak) in attritional profiles but not in catastrophic ones. Detecting such a rise and demonstrating its statistical reality will probably require samples larger than the ones palaeontologists or archaeologists can usually obtain.

3. Very young ungulates will generally be underrepresented (in contrast to their live abundance) in mortality profiles obtained from skeletal remains, whether these are recent or fossil. The reason is that the bones of very young individuals are more fragile than those of older ones. In fossil sites where bone preservation is good, so that post-depositional destruction was probably minimal, the underrepresentation of very young individuals is most likely due to pre-depositional destruction or removal by carnivores and scavengers. It follows that sites in which very young individuals are abundant must either be ones at which carnivores and scavengers were absent, or ones to which they took bones but did not consume them. In the case of a hominid (archaeological) site where bones of very young individuals are abundant, the implication is either that the people were able to locate the carcasses of very young individuals before other predators, or that they actively hunted the very young individuals. A priori, the second alternative seems more likely.

4. Predation on ungulates may produce either attritional or catastrophic mortality profiles. Attritional mortality profiles will tend to characterize long-standing predator-prey relationships. It is probable that only recent man regularly produces catastrophic prey profiles. Predation that leads to catastrophic profiles must be restrained, voluntarily, or otherwise, if it is not to reduce or extinguish prey populations.

5. The interpretation of mortality profiles derived from fossil samples is dependent upon the availability of sound contextual information. Thus, the conclusion that the giraffid and *Damalacra* individuals in the Langebaanweg channel fills died by drowning during flash or peak floods is based both on the mortality profiles that characterize the samples and on the sedimentary facies in which they occur. The lack of contextual information for most of the bones collected at Elandsfontein makes it difficult, if not impossible, to interpret the Elandsfontein mortality profiles meaningfully.

6. Mortality profiles based on fossil samples may be useful for establishing basic biological facts about certain species that are difficult to establish by observation of live populations. Thus the fact that mortality profiles of *Raphicerus* from a wide variety of sites always exhibit the same down-staircase form, in spite of the fact that mortality at some (?most) of the sites was probably attritional, implies that *Raphicerus* females commonly bear more than one young per year. More generally, many fossil samples are probably derived from populations in which short-term fluctuations in overall size and age structure have balanced each other out, so that the survivorship and mortality patterns that the samples exhibit are the long-term ones that biologists seek in order to gauge the ecological status or health of living populations.

7. In theory, the crown height distributions of a fossil population that was characterized by seasonally restricted birth and death will exhibit patterned multimodality reflecting the discontinuity of the underlying age distribution. In practice, the discovery of convincing multimodality will require much larger samples than most palaeontologists or archaeologists generally obtain, preferably from species in which dental crowns were very high relative to potential individual lifespan.

8. In fossil samples, sex ratios are generally more difficult to establish and more difficult to interpret than age profiles. Measurements on weight-bearing bones that are likely to reflect size differences provide the most widely applicable means of estimating the sex ratio in fossil ungulate samples.

9. Although ageing animals from skeletal remains can be problematic, for many high-crowned ungulate species ageing from teeth using quadratic formulae such as those employed in this paper will probably provide age profiles that are reasonably accurate. The wider application of mortality profile analysis in palaeontology and archaeology is not limited by problems of ageing but by the frequent lack of sufficiently large samples.

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